# PHYLOGENY, TAXONOMY, AND BIOGEOGRAPHY OF EXTANT SILKY LACEWINGS (INSECTA: NEUROPTERA: PSYCHOPSIDAE)

By

John D. Oswald

Paul M. Marsh
Editor

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# Extant Silky Lacewings (Insecta: Neuroptera: Psychopsidae)

by

## John D. Oswald

Department of Entomology
National Museum of Natural History, NHB 165
Smithsonian Institution
Washington, D.C. 20560

Abstract. The world genera of the family Psychopsidae are revised based on a comparative morphological assessment of adults of 21 (of 26) extant silky lacewing species. Two subfamilies and five genera are recognized. The subfamily Zygophlebiinae contains three African genera, *Silveira*, *Cabralis*, and *Zygophlebius*; the subfamily Psychopsinae contains the genera *Balmes*, from southeast Asia, and *Psychopsis*, from Australia. A generic key and full taxonomic treatments of all supraspecific taxa are presented, together with a synonymical catalog of extant species. Three new species are noted. A novel male/female copulatory mechanism is described; and several hypotheses are advanced regarding the functional morphology of the male and female terminalia. A cladistic analysis of the 21 examined species using 60 adult morphological characters demonstrates the holophyly of all recognized supraspecific taxa. The five recognized genera are cladistically related as follows: ([*Silveira* + (*Cabralis* + *Zygophlebius*)] + [*Balmes* + *Psychopsis*]). Alternative classifications of the family are discussed, particularly with regard to the Australian species. The biogeography of extant psychopsids is discussed. The distribution and cladogeny of living silky lacewings is consistent with a Gondwanan origin of the extant members of the family. The present occurrence of *Balmes* species in southeast Asia is best explained by either (1) the northwesterly dispersal of an Australian, probably Tertiary, ancestor through the Malay Archipelago or (2) the northerly rafting of a Mesozoic ancestor on a rift fragment of northeastern Gondwanaland.

## INTRODUCTION

The neuropterous family Psychopsidae, or "silky lacewings," contains 26 extant species (including three undescribed, see Appendix 1) and a variety of fossil forms ranging in age from Tertiary to Triassic (Table 5, page 48). This work treats the phylogeny, taxonomy, biogeography, and several aspects of the functional morphology of living psychopsids.

Because of the absence of silky lacewings from Europe and adjacent land areas, psychopsids came to the attention of western science at a relatively late date. The first described species, the attractive *Psychopsis mimica* from Australia, was initially characterized by Edward Newman in 1842, and more completely described the following year (Newman, 1843). Newman's implicit and appropriate comparison of *mimica* to a colorfully banded lepidopteran is memorialized in his generic name *Psychopsis*, derived from the Greek words *psyche*, butterfly, and *opsis*, appearance. In 1889, Friedrich Brauer described the first African psychopsid, *zebra*. Two years later Robert McLachlan (1891) re-

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corded the first silky lacewing from southeastern Asia, *birmanus*, and established the presence of psychopsids in the last of the three disjunct geographies—Australia, sub-Saharan Africa, and southeast Asia—which currently comprise the tripartite distribution of the living members of this family.

Handlirsch (1906-1908) recognized the distinctiveness of the genus *Psychopsis* within the broad concept of the family Hemerobiidae then current and erected for it a new subfamily, the Psychopsinae, which was subsequently adopted by several contemporaries, e.g., Banks (1913) and Nakahara (1914). Navás (1910), apparently then unaware of all earlier work on this group, independently proposed two generic names, *Zygophlebius* and *Balmes*, to contain three new species (one each from Africa, Australia, and southeast Asia) that are now recognized as psychopsids. Navás placed his genera in a new hemerobiid tribe, the Zygophlebini.

In the years following his 1910 paper, Navás described several additional new psychopsids in a series of general papers (e.g., Navás, 1910, 1912a, 1912b) and one revisionary work, the "Ensayo monográfico de la familia de los Sicópsidos." Although the latter work was not published until 1917 (Navás, 1917), it was presented orally at the Valladolid Congress of the Asociación Española para el Progreso de las Ciencias in October, 1915. Several aspects of this work are significant: (1) it contained the first elevation of psychopsids to family rank—although, the family name "Psychopsidae" itself was first published independently by Tillyard (1916:271), (2) it represented the first comprehensive, worldwide, review of the family, recognizing eight genera, 13 species, and three varieties, and (3) it firmly established alar characters, principally venation and wing patterning, as the principal diagnostic and taxonomic traits used in the early differentiation of psychopsid taxa—an emphasis which was maintained throughout the subsequent revisions of Tillyard ([1919a]; Australia), Krüger (1922; world), and Kimmins (1939; world).

More recently, Tjeder's (1960) revision of the southern African psychopsid fauna conclusively demonstrated the taxonomic utility of male and female terminalic characters at all hierarchical levels within the family. Tjeder's expansion of the taxonomic character base in psychopsids to include terminalic traits was a major advance and paral-

leled concurrent trends in other neuropterous families. Subsequently, New ([1989a]) made extensive use of terminalic traits to diagnose Australian psychopsids.

The present work builds upon this 150-year history. The major new contribution contained here is the first detailed hypothesis of interspecific and intergeneric relationships within the family. This hypothesis is based upon a cladistic analysis of 60 characters (mostly terminalic) scored for 21 (of 26) living psychopsid species. The relative phylogenetic relationships inferred from this analysis are used (1) as the basis for a new generic and suprageneric classification of the family and (2) to interpret the biogeographic history of living silky lacewings and to account for their presently tripartite distribution. The descriptive aspects of this work are limited to taxa of generic and suprageneric rank. Consequently, full taxonomic treatments are provided only for the two subfamilies and five genera recognized here. A comprehensive synonymical catalog of extant psychopsid species, however, has been provided (Appendix 1), and synapomorphic characters supporting intrageneric clades among the examined species are included in the cladistic analysis. Readers are referred to the revisionary works of Tjeder (1960) and New ([1989a]) for species-level taxonomic treatments of African and Australian psychopsids respectively. The interspecific taxonomy of southeast Asian psychopsids requires additional study.

## ACKNOWLEDGMENTS

## MATERIALS AND METHODS

**Material.**—This study was based on the examination of approximately 650 specimens representing 21 of the 26 known extant psychopsid species. The individuals and institutions who/which loaned this material are listed below under "Collection Acronyms."

**Terminalia Preparation.**—The following general sequence was used to prepare male and female terminalia: (1) remove abdomen from specimen [whole or only apical segments (ca. somites 6+)], (2) immerse overnight in cold 10% KOH to soften, digest, and hydrate, (3) rinse in 70% ethyl alcohol [EtOH], (4) [optional] stain in saturated solution of 70% EtOH and Chlorozol Black for approximately one minute, then rinse in 70% EtOH, (5) transfer to glycerin for dissection and examination.

Rinsing is facilitated by use of a syringe containing EtOH and a fine, bent-tipped needle. Removal of the gonarcus/mediuncus/9th gonocoxite complex from the abdominal apex of the male facilitates detailed examination and illustration of both this complex and the tergal and sternal elements which enclose it. Removal can be accomplished using a pair of jewelers' forceps and a fine probe to part the membranes joining these structures. Examination of female terminalic structures—particularly the bursa, spermatheca, posterior abdominal chamber, and various sternal structures—is greatly aided by cutting the abdominal body wall in a horizontal plane at approximately the level of the spiracles. To accomplish this, first trim the abdomen to contain approximately somites 6+. Then, with a fine pair of scissors, cut horizontally through the body wall from the pleural membrane to the distal apex of the ectoproct. With similar cuts made on both sides of the abdomen, the dorsal half of the abdomen can be bent back and the remaining connection severed. Careful cuts will avoid damage to the bursa, its glands, the spermatheca, and the posterior abdominal chamber.

**Illustrations.**—Terminalic drawings were prepared using a drawing tube attached to a dissecting microscope from structures either (1) completely embedded in glycerin jelly, or (2) partially embedded in petroleum jelly and covered with liquid glycerin. The excellent illustrations found in Tjeder (1960) are frequently cited herein to avoid excessive duplication of artwork. References to figures contained in Tjeder and other published works are cited as "fig." [lower case f]; figures contained in this work are cited as "Fig." [upper case F].

**Terminology.**—The morphological terminology used here generally follows that of Tjeder (1960) and New ([1989a]). A number of terminological differences, however, occur in (1) the male gonarcus/mediuncus/9th gonocoxite complex, and (2) the female ventral terminalia. A cross-reference guide to these differences is given below. Justifications of the terms used here are given in the text, particularly in the discussions of characters used in the cladistic analysis and under the heading "Functional Morphology of Male and Female Terminalia: Morphological Observations." Discussions of the terminology used for the gonarcus are given in Oswald (1988:396) and Oswald (1993: 155-157).

Cross-reference guide to terminalic terminology (Format: Tjederian term = Current term [(M)ale/(F)emale]): arcessus = mediuncus [M]; entoprocessus = extrahemigonarcal process [M]; glandulae accessoriae = bursal accessory glands [F]; gonapophysis lateralis = 9th gonocoxite [F]; paramere = 9th gonocoxite [M]; pregenitale = 8th sternite [F]; spermatheca = bursa (membranous portion) + spermatheca (sclerotized portion) [F].

**Collection Acronyms.**—**AMS**—Australian Museum, Sydney, NSW Australia; **BMNH**—The Natural History Museum, London, England; **CAS**—California Academy of Sciences, San Francisco, CA, USA; **CUIC**—Cornell University Insect Collection, Ithaca, NY, USA; **DANSW**—Agricultural Scientific Collections Trust (NSW Dept. Agric.), Rydalmere, NSW, Australia; **EMAU** - Zoologisches Museum, Ernst-Moritz-Arndt-Universität, Greifswald, Germany; **FSCA**—Florida State Collection of Arthropods, Gainsville, FL, USA; **MCZ**—Museum of Comparative Zoology, Cambridge, MA, USA; **MINTER**—Les Minter private

collection, Pietersburg, South Africa; **MRAC**— Musée Royal de l'Afrique Centrale, Tervuren, Belgium; **NCIP**—National Collection of Insects, Pretoria, South Africa; **NHMW**—Naturhistorisches Museum, Wien, Austria; **NMB**—Natural History Museum, Bulawayo, Zimbabwe; **NMK**—National Museum of Kenya, Nairobi, Kenya; **USNM**—National Museum of Natural History, Washington, D.C., USA; **NMSA**—Natal Museum, Pietermaritzburg, South Africa; **QMB**—Queensland Museum, South Brisbane, Queensland, Australia; **RNHL**—Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; **SAMA**— South Australian Museum, Adelaide, South Australia, Australia; **SAMC**—South African Museum, Cape Town, South Africa; **SMWW**—State Museum, Windhoek, Namibia; **UQIC**—University of Queensland, St. Lucia, Queensland, Australia; **UZIL**—Museum of Zoology and Entomology, Lund University, Lund, Sweden; **ZMHB**—Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; **ZSM**— Zoologische Staats-sammlung, München, Germany.

<center>TAXONOMIC TREATMENTS</center>

<center>Family PSYCHOPSIDAE Handlirsch</center>

Psychopsinae Handlirsch [1906]:42 [As a subfamily of Hemerobiidae. Type genus: *Psychopsis* Newman, 1842.].—Banks, 1913:211 [nomenclature]; Nakahara, 1914:491 [nomenclature].
Psychopsini.—Navás, 1912b:194 [As a tribe of Hemerobiidae. Note: Navás's proposal of this name was apparently independent of Handlirsch's prior use of the name Psychopsinae. Navás proposed the name Psychopsini to replace his earlier tribal name Zygophlebini (based on *Zygophlebius* Navás, 1910), subsequent to his discovery of the existence of the older generic name *Psychopsis*.].
Psychopsidae.—Tillyard, 1916:271 [nomenclature]; Navás, 1917 [taxonomy]; Tillyard, [1919a] [taxonomy]; Krüger, 1922 [taxonomy]; Kimmins, 1939 [taxonomy]; Tjeder, 1960 [taxonomy]; New, [1989a] [taxonomy].
Balmesini Navás, 1917:207 [As a tribe of Psychopsidae. Type genus: *Balmes* Navás, 1910.].
Psychopsididae [sic].—Martynova, 1949:161 [nomenclature].

**Diagnosis.**—Medium-sized to large neuropterans (forewing length 10-35 mm) readily distinguished by the presence of a forewing and hind wing venational formation called the "vena triplica"

(Fig. 32, vt). In this formation the subcostal and R1 spaces run parallel, and are subequal in width, from near the base of the wing to a common (or nearly common) distal point (the "anastomosis"; Fig. 32, ams) where each space is either constricted (by an interposed crossvein) or terminated (by brief vein fusion), and beyond (distal to) which point the parallel, subequal, nature of the spaces is not apparent. Other characteristic forewing traits include: (1) an unusually broad costal space, its width at least twice the width of the "vena triplica" near the "anastomosis," i.e., in the "pterostigmal region," (2) the presence of only one forewing nygma, located basally between veins R and M, (3) the complete absence of pterostigmata, and (4) the presence of at least four (usually >10) crossveins traversing the subcostal space between its base and the "anastomosis."

**Description.**—In the following treatment familial synapomorphies are indicated by bracketed character numbers (see Phylogenetic Analysis: Characters below). See also the discussions under the heading "Functional Morphology of Male and Female Terminalia." **Head**: compound eyes prominent; ocelli absent; 2 or 3 ocellar/cranial pulvinae usually present (all lost in *P. coelivaga*); antennae short, moniliform; toruli with one or two antennifers; maxillary palpi 5-segmented; labial palpi 3-segmented, ultimate labial palpomeres each bearing a palpimacula; mandibles well developed, slightly asymmetrical. **Thorax**: Pterothorax macropterous; wings generally broadly triangular; margins trichosorate; membrane fully microtrichose, but not macrotrichose; hind wing somewhat smaller than forewing. Forewing distinctly patterned, sometimes with brightly colored patches; humeral plate prominent, sometimes elongate; costal space very broad throughout, width in "pterostigmal region" >2 times the combined width of the adjacent Sc and R1 spaces [8]; pterostigma absent; costal gradate series present [6] (occasionally secondarily reduced or lost); proximal humeral trace recurrent and pectinately branched; subcostal space with more than four crossveins (but usually >10) [5]; longitudinal veins and costal veinlets densely macrotrichose. Legs cursorial; paired tibial spurs present; tarsi 5-segmented; pretarsus biclawed, arolium present, simple.

**Male Terminalia** (Figs. 1, 18).—**8th Somite**: tergite narrowed, hemiannular; sternite hemiannular to moderately produced posteriorly;

spiracles opening through ventrally prolonged margins of tergite [10] (secondarily free in several species). **9th Somite**: tergite arcuate, narrowed dorsally, expanded and elongated ventrally; tergal antecosta prominent, especially ventrolaterally, distal (ventral) ends articulated to anterolateral margins of 9th sternite [14]; sternite variously modified, usually somewhat reduced, composed principally of a pair of rigid lateral longitudinal costae [17], with various degrees of adjacent sclerotization, apex frequently emarginate, lateral costae articulated proximally to antecosta of 9th tergite [14], lateral costae continued internally as a pair of short apodemes [15]. **Ectoprocts**: free dorsomedially, doubly (two species; e.g., Fig. 21) or singly lobed distally, trichobothriate callus cercus always present. **Gonarcus** (Fig. 23): a prominent arcuate framework serving as the articulatory base of the mediuncus and 9th gonocoxites; extragonopons, extrahemigonarcus, and intrahemigonarcus prominent; intragonopons absent or poorly developed; extragonopons generally protruded beyond extrahemigonarcus in lateral view. **Mediuncus** (=arcessus of Tjeder and New): always present, proximal end articulated to posterior margin of extragonopons by means of a transverse flexion line; curvature variable; apex simple or bifid; apodeme of mediuncal adductor muscle always distinct [36]; proximoventral surface of mediuncus associated with a pair (sometimes fused sagittally) of accessory sclerites developed in adjacent gonosaccal membrane [37]. **9th Gonocoxites**: always present and paired; proximal ends articulated to posteroventral angles of extrahemigonarcus; distal ends fused at abdominal midline [23] (except in *P. coelivaga*) to form a more or less rigid arch joining the extrahemigonarcus. **Miscellaneous**: hypandrium internum and subanale always present.

**Female Terminalia** (Figs. 43–44).—**7th Somite**: tergite hemiannular, unmodified; sternite more or less hemiannular overall, posterior margin with a sagittal emargination and/or depression [40]; copulatory fovea present [42]. **8th Somite**: tergite narrowed, lateral extremities greatly prolonged ventrally, posterior margin fused for much of its length (especially laterally and ventrolaterally) to anterior margin of 9th tergite [46]; spiracles opening through ventrally prolonged margins of tergite;

sternite always present, conformation variable (narrowly rectangular [44], triangular, trapezoidal, or compact and lobed), fused to 7th sternite in several species. **9th Somite**: tergite narrowed dorsally, greatly expanded ventrally, posteroventral expansion subtending ectoproct posteriorly; contralateral tergal margins adpressed ventrally; posteroventral tergal surfaces inwardly revolute and pilose [48]; tergal antecosta prominent for much of its length, particularly laterally and ventrolaterally, and giving rise to a pair of short broad apodemes (Fig. 43, ala) above spiracles of 8th somite [47]; a pair of slender inconspicuous apodemes (Fig. 43, da) issuing from near dorsal angles of posteroventral lobes of tergite [49]; subgenitale present, a subrectangular plate bearing a pair of small, free, lateral lobes. **Ectoprocts**: proximolateral margins more or less fused to 9th tergite, development of suture in this area variable, free on sagittal midline of abdomen, but parasagittal margins joined dorsally by a narrow membranous rift which severely restricts lateral ectoproctal motion. **9th Gonocoxites**: present, spathulate [50], each with a prominent longitudinal costa [51], at least some cochleariform suprastylar setae present [54]; 9th gonocoxal styli present, each bearing a field of short stout "digging" setae [55]. **Internal Structures**: bursa a large membranous sac, its ventral margins confluent with the adpressed dorsal edges of an elongate, sclerotized, slit-entry spermatheca; colleterial gland present, one pair of dorsodistal bursal accessory glands normally present (see Character 56 for variants); posterior abdominal chamber present [60]. **Miscellaneous**: subanale always present.

**Natural History and Immature Stages**.—See individual generic treatments below.

**Distribution**.—Range tripartly disjunct: southern half of Africa (predominantly south of the Equator), southeastern Asia (limits of distribution poorly known, reported from Burma, southern China, Laos, and Taiwan), and Australia (widespread, but records predominantly eastern).

**Included Taxa**.—Two subfamilies: Zygophlebiinae (three genera, nine species) and Psychopsinae (two genera, 17 species). For additional discussion of family classification see "Phylogenetic Analysis: Classification" below. All extant species are cataloged in Appendix 1.

## KEY TO SUBFAMILIES AND GENERA OF PSYCHOPSIDAE

1       Distribution: Africa (Fig. 54); Male: apex of mediuncus simple (Fig. 4); Female: spermatheca bearing a pair of
        hollow ventrolateral lobes (Fig. 46, vll) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . (Zygophlebiinae) **2**
        Distribution: Australia or southeastern Asia (Fig. 54); Male: apex of mediuncus emarginate or bifid (Fig. 27);
        Female: spermatheca lacking hollow ventrolateral lobes, but solid apodemal plates (Fig. 48, lap) may be
        present ventrolaterally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . (Psychopsinae) **4**
2(1)    Head: vertex bearing 3 well-developed ocellar/cranial pulvinae (Tjeder, 1960:175, fig. 341); Female: hollow
        ventrolateral lobes of spermatheca slender (Tjeder, 1960:179, fig. 365) . . . . . . . . . . . . . . . . . . *Silveira* Navás
        Head: vertex bearing 2 well-developed ocellar/cranial pulvinae [anteromedian pulvinus absent] (Tjeder,
        1960:192, fig. 405); Female: ventrolateral lobes of spermatheca broad (Fig. 46) . . . . . . . . . . . . . . . . . . . . . . . **3**
3(2)    Forewing: bearing dark spots on a white ground (Tjeder, 1960:199, fig. 434A); Hind Wing: crossveins closing
        "vena triplica" distally not dark brown; Male: apex of mediuncus strongly decurved (Fig. 19); Female: bursa
        without corniform diverticulae (Tjeder, 1960:203, fig. 448) . . . . . . . . . . . . . . . . . . . . . . . . *Cabralis* Navás
        Forewing: bearing transverse bars proximally on a yellowish or hyaline ground [wing lightly mottled in zns1,
        bars inconspicuous] (Tjeder, 1960:193, fig. 412); Hind Wing: crossveins closing "vena triplica" distally dark
        brown; Male: apex of mediuncus recurved (Fig. 14); Female: bursa with a pair of corniform diverticulae (Fig.
        47, cd) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Zygophlebius* Navás
4(1)    Hind Wing: bearing a prominent dark macula on, beyond, or below anastomosis of "vena triplica" [Australia]
        . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Psychopsis* Newman
        Hind Wing: dark distal macula lacking [Southeast Asia. The Australian species *gallardi*, regarded here as
        Psychopsinae incertae sedis, will also key here.] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Balmes* Navás

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## Subfamily ZYGOPHLEBIINAE Navás

Zygophlebini Navás, 1910:82 [As a tribe of
    Hemerobiidae. Type genus: *Zygophlebius* Navás,
    1910].—Navás, 1917 [taxonomy].

**Diagnosis**.—Cladistic analysis character num-
bers bracketed ([xx]), synapomorphies asterisked
(*). **Head**: Vertex bearing 2 (*Cabralis* and
*Zygophlebius*) or 3 (*Silveira*) well-developed ocel-
lar/cranial pulvinae [1]; antennal toruli each with
2 antennifers, 1 medial and 1 lateral [2*, unique].
**Male Terminalia**: Anterolateral apodemes of 9th
sternite continuing in line with proximal ends of
lateral costae [15]; 9th Gonocoxites without true
superprocesses [24]; apex of mediuncus simple
[32]; apodeme of adductor muscle of mediuncus
inserting proximoventrally on floor of mediuncus
[36]. **Female Terminalia**: Suprastylar setae of 9th
gonocoxite <50% (*Silveira*) or >50% (*Cabralis* and
*Zygophlebius*) cochleariform [54]; spermatheca
bearing a pair of ventrolateral lobes [58*, unique].
    **Distribution**.—Southern half of Africa.
    **Included Taxa**.—*Silveira* (four species), *Cabralis*
(two species, including one undescribed), and
*Zygophlebius* (three species, including one
undescribed) [see Appendix 1].

## Genus **SILVEIRA** Navás

Figs. 1-5, 39, 41

*Silveira* Navás, 1912b:196 [Type species: *Silveira
    marmoratus* Navás, 1912b:196 (=*Psychopsis marshalli*
    McLachlan, 1902), by monotypy. Etymology: from
    the surname of Gonzalo Silveira, S. J., see Navás,
    1912b:196. Gender: Masculine (implied from the
    original combination *Silveira marmoratus*, Art.
    30d).].—Navás, 1917 [taxonomy]; Kimmins, 1939
    [taxonomy]; Tjeder, 1960 [taxonomy].
*Psychophasis* Krüger, 1922:44 [Type species: *Psychopsis
    marshalli* McLachlan, 1902:234, by original designa-
    tion. Etymology: unexplained, probably Psycho-
    (from Gr. *psyche*, butterfly) + -phasis (from Gr. *phasis*
    [fem.], appearance). Gender: Feminine.].—Kimmins,
    1939 [synonymy].

**Diagnosis**.—Cladistic analysis character num-
bers bracketed ([xx]), synapomorphies asterisked
(*). **Head**: Vertex bearing 3 well-developed ocellar/
cranial pulvinae [1]. **Wings**: Forewing without light
brown transverse bars [4]; forewing costal gradate
series well developed [6]; hind wing without a
dark distal macula [9]. **Male Terminalia**: 8th ster-
nite without a posteromedian lobe [11]; 9th tergite
without free posteroventral processes [12]; 9th
sternite narrow and parallel sided in ventral view
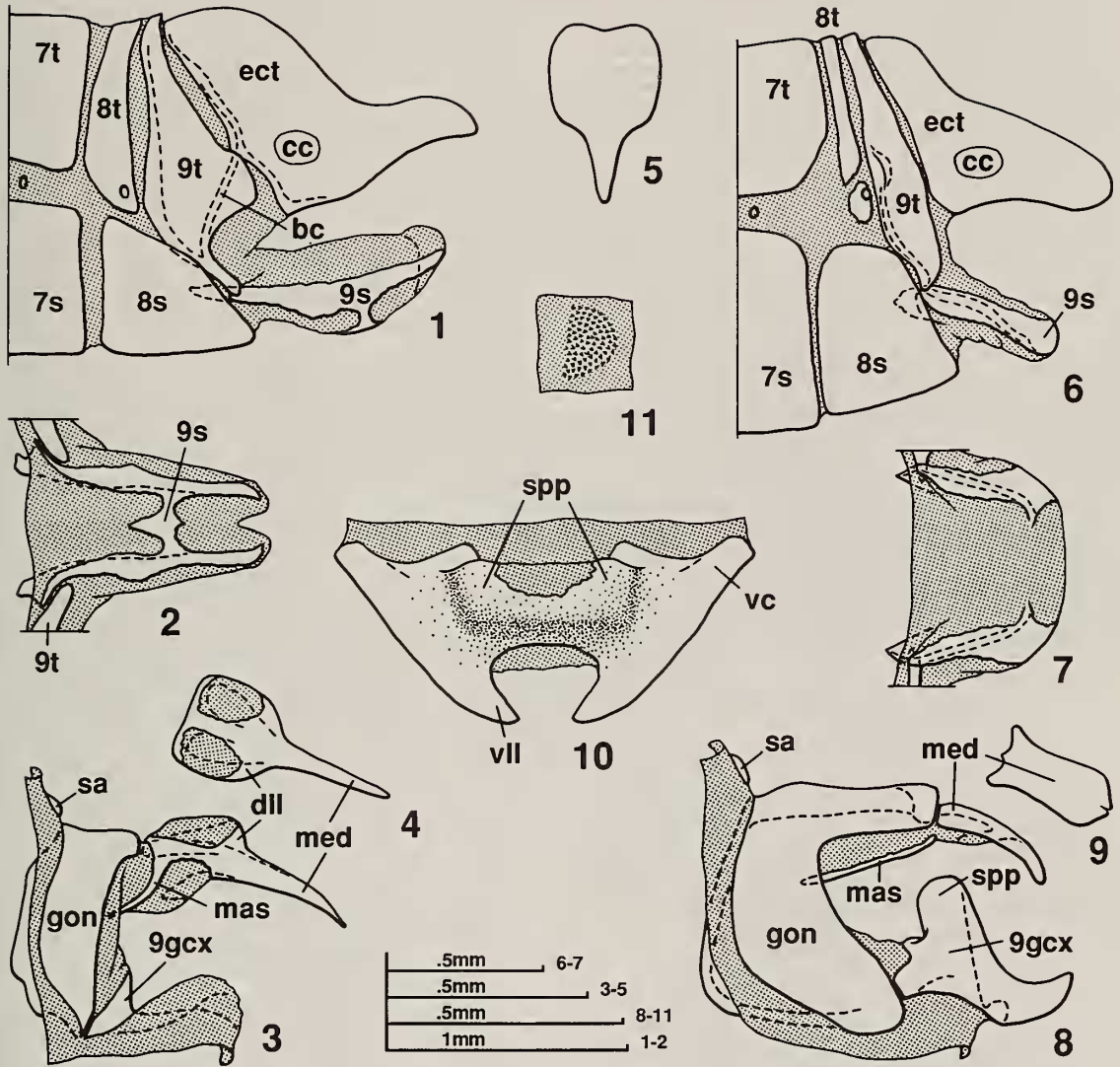
Figs. 1-11. 1-4, *Silveira marshalli*, male. 1, abdominal apex, lateral. 2, 9th sternite, ventral. 3, gonarcus and 9th gonocoxites, lateral. 4, mediuncus, dorsal. 5, *Silveira rufus*, male mediuncus, dorsal outline. 6-11, *Balmes birmanus*, male. 6, abdominal apex, lateral. 7, 9th sternite, ventral. 8, gonarcus and 9th gonocoxites, lateral. 9, mediuncus, dorsal. 10. 9th gonocoxites, dorsal. 11, spiculate lobe of gonosaccal membrane, lateral. Abbreviations: **7s, 8s, 9s**, sternites; **7t, 8t, 9t**, tergites; **9gcx**, 9th gonocoxite; **bc**, brace costa; **cc**, cercal callus; **dll**, dorsolateral lobe; **ect**, ectoproct; **gon**, gonarcus; **mas**, mediuncal accessory sclerite; **med**, mediuncus; **sa**, subanale; **spp**, superprocessus; **vc**, ventral costa; **vll**, ventrolateral lobe.

[16*, unique], its apex shallowly emarginate [19*, homoplasious]; 9th Gonocoxites: ventral costae long and prominent [21], dorsolateral sclerotized plates not flared laterally [22], superprocesses absent [24]; mediuncus weakly decurved [33], not recurved [34]; gonosaccal membrane without spiculate lobes [39]. **Female Terminalia**: Posterior margin of 7th sternite medially depressed and emarginate [40]; 7th and 8th sternites unfused [43]; 8th sternite narrow and transverse [44]; 9th Gonocoxites: each gonocoxite bearing a single longitudinal row of stiff setae below the gonocoxal costa [52*, unique], without a compact aggregation of setae borne adjacent to insertion of stylus [53], suprastylar setae <50% cochleariform [54]; bursa without lateral corniform diverticulae [57]; hollow ventrolateral lobes of spermatheca narrow in lateral view [58*, unique].

**Natural History and Immature Stages.**—No published data. Larvae of *marshalli* have been reared to 2nd instar by L. Minter (pers. comm.).

**Distribution.**—Southern half of Africa (Angola, Botswana, Namibia, Republic of South Africa [Cape Prov., Transvaal], Zaire, Zimbabwe).

**Species.**—Four (see Appendix 1; Key: Tjeder, 1960:174-175).

## Genus **CABRALIS** Navás
### Figs. 17-20

*Cabralis* Navás, 1912a:109 [Type species: *Cabralis gloriosus* Navás, 1912a:110, by monotypy. Etymology: unexplained, unknown. Gender: Masculine (implied from the original combination *Cabralis gloriosus*, Art. 30d).].—Navás, 1917 [taxonomy]; Kimmins, 1939 [taxonomy]; Tjeder, 1960 [taxonomy].

**Diagnosis.**—Cladistic analysis character numbers bracketed ([xx]), synapomorphies asterisked (*). **Head**: Vertex bearing 2 well-developed ocellar/cranial pulvinae [1]. **Wings**: Forewing without light brown transverse bars [4]; forewing costal gradate series well developed [6]; hind wing without a dark distal macula [9]. **Male Terminalia**: 8th sternite with an inconspicuous posteromedian lobe [11]; 9th tergite margins produced posteroventrally as a pair of free processes [12*, unique]; 9th sternite not narrow and parallel sided in ventral view [16], its apex rounded, not emarginate [19]; 9th Gonocoxites: ventral costae long and prominent [21], dorsolateral sclerotized plates not flared laterally [22], superprocesses absent [24]; mediuncus strongly decurved [33*, unique], not recurved [34];

gonosaccal membrane without spiculate lobes [39]. **Female Terminalia**: Posterior margin of 7th sternite deeply depressed and emarginate medially [40]; 7th and 8th sternites not fused [43]; 8th sternite a compact median sclerite [44]; 9th Gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa [52], without a compact aggregation of setae borne adjacent to insertion of stylus [53], suprastylar setae >50% cochleariform [54]; bursa without lateral corniform diverticulae [57]; hollow ventrolateral lobes of spermatheca broad in lateral view [58].

**Natural History and Immature Stages.**—No published data. Larvae of *C. gloriosus* have been reared to 2nd instar by L. Minter (pers. comm.).

**Distribution.**—Southeastern Africa (Mozambique, Republic of South Africa [Transvaal], Zaire, Zimbabwe).

**Species.**—Two, including one undescribed [=cns1] (see Appendix 1).

## Genus **ZYGOPHLEBIUS** Navás
### Figs. 12-16, 43-47

*Zygophlebius* Navás, 1910:82 [Type species: *Zygophlebius leoninus* Navás, 1910:83, by subsequent designation by Navás, 1917:200, who designated *Psychopsis zebra* Brauer, 1889:102, a name not originally included in *Zygophlebius*, but at the same time placed the originally included species *Z. leoninus* (as subspecies leonina [sic]) as a synonym of *P. zebra*, Art. 69a(v) (see discussion in Oswald, 1989). Incorrect Type Species Designation: *Zygophlebius verreauxinus* Navás, 1910:84, by Tillyard, [1919a]:760. Etymology: Zygo- (from Gr. zygon, yoke) + -phlebius (from Gr. *phleps* or *phlebos* [fem.], vein), see Navás, 1910:82. Gender: Masculine, Art. 30a(iii).].—Navás, 1917 [taxonomy]; Tillyard, [1919a]:759 [nomenclature]; Oswald, 1989 [nomenclature].

*Notopsychops* Tillyard, [1919a]:759 [Type species: *Psychopsis zebra* Brauer, 1889:102, by original designation. Etymology: unexplained, probably Noto- (from L. *noto*, to mark) + -psych- (from Gr. *psyche*, butterfly) + -ops (from Gr. *ops* [fem.], countenance). Gender: Masculine, Art. 30a(ii). Note: Proposed unnecessarily as a replacement name for *Zygophlebius* sensu Navás, 1917, see discussion in Oswald, 1989:139.].—Kimmins, 1939 [taxonomy]; Tjeder, 1960 [taxonomy]; Oswald, 1989 [synonymy].

*Psychomorphe* Krüger, 1922:44 [Type species: *Psychopsis zebra* Brauer, 1889:102, by original designation. Etymology: unexplained, probably Psycho- (from Gr. *psyche*, butterfly) + -morphe (from Gr. *morphe* [fem.], form). Gender: Feminine.].—Kimmins, 1939 [synonymy].
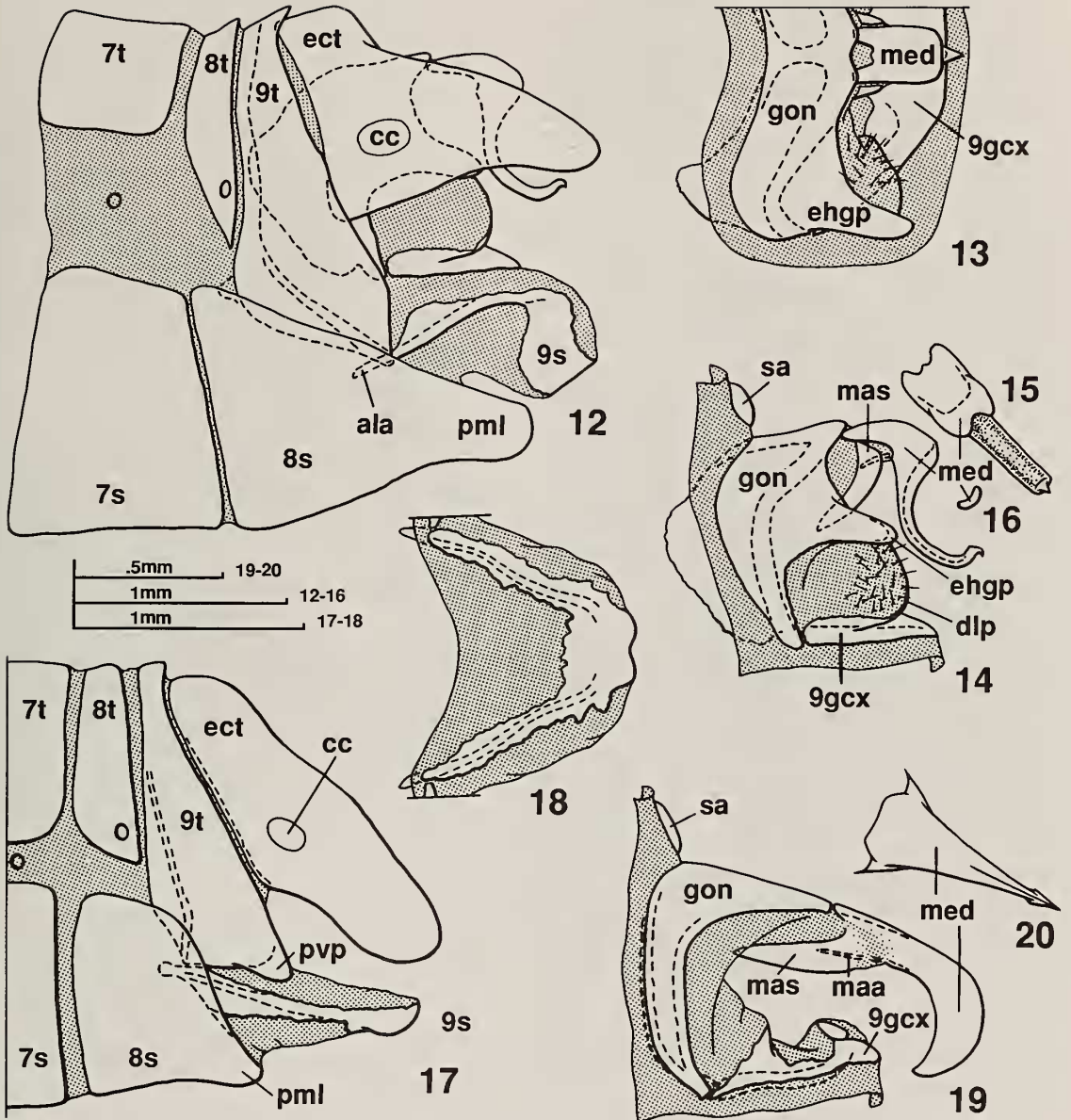
Figs. 12-20. 12-16, *Zygophlebius leoninus*, male. 12, abdominal apex, lateral. 13, gonarcus and 9th gonocoxites, dorsal. 14, same, lateral. 15, mediuncus, dorsal. 16, same, distal cross-section. 17-20, *Cabralis gloriosus*, male. 17, abdominal apex, lateral. 18, 9th sternite, ventral. 19, gonarcus and 9th gonocoxites, lateral. 20, mediuncus, dorsal. Abbreviations: 7s, 8s, 9s, sternites; 7t, 8t, 9t, tergites; 9gcx, 9th gonocoxite; cc, cercal callus; ala, anterolateral apodeme; dlp, dorsolateral plate; ect, ectoproct; ehgp, extrahemigonarcal process; gon, gonarcus; maa, mediuncal adductor apodeme; mas, mediuncal accessory sclerite; med, mediuncus; pml, posteromedian lobe; pvp, posteroventral lobe; sa, subanale.

*Nothopsychops.*—Tjeder, 1960:173 and figure legends for "*Notopsychops zebra*" (=*leoninus*) [An incorrect subsequent spelling of *Notopsychops*].

**Diagnosis.**—Cladistic analysis character numbers bracketed ([xx]), synapomorphies asterisked (*). **Head:** Vertex bearing 2 well-developed ocellar/cranial pulvinae [1]. **Wings:** Forewing with light brown transverse bars [4*, unique]; forewing costal gradate series well developed (*zebra, leoninus*), or secondarily reduced (zns1) [6]; hind wing with a minute dark mark directly on the "anastomosis" [9*, unique]. **Male Terminalia:** 8th sternite with a posteromedian lobe [11]; 9th tergite without free posteroventral processes [12]; 9th sternite not narrow and parallel sided in ventral view [16], its apex shallowly emarginate (*zebra, leoninus*) or rounded (zns1) [19]; 9th Gonocoxites: ventral costae long and prominent [21], dorsolateral sclerotized plates flared laterally [22*, unique], superprocesses absent [24]; mediuncus distally recurved [34*, unique]; gonosaccal membrane without spiculate lobes [39]. **Female Terminalia:** Posterior margin of 7th sternite medially depressed and emarginate, and bearing a sagittal process (minute in zns1) [40*, unique]; 7th and 8th sternites not fused [43]; 8th sternite a compact median sclerite [44]; 9th Gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa [52], without a compact aggregation of setae borne adjacent to insertion of stylus [53], suprastylar setae >50% cochleariform [54]; bursa with lateral corniform diverticulae [57*, unique]; hollow ventrolateral lobes of spermatheca broad in lateral view [58].

**Natural History and Immature Stages.**—No published data. Larvae of *leoninus* and zns1 have been reared, respectively, to 2nd and 3rd instar by L. Minter (pers. comm.).

**Distribution.**—Southern half of Africa (Angola, Kenya, Malawi, Mozambique, Republic of South Africa [Transvaal], Swaziland, Tanzania, Uganda, Zaire, Zambia, Zimbabwe).

**Species.**—Three, including one undescribed [=zns1] (see Appendix 1; no recent authoritative species key exists).

### Subfamily PSYCHOPSINAE Handlirsch

For synonymical listing see family treatment above.

**Diagnosis.**—Cladistic analysis character numbers bracketed ([xx]), synapomorphies asterisked (*). **Head:** Vertex bearing 2 ocellar/cranial pulvinae

(the 3rd, medioventral, occasionally vestigial; all pulvinae absent in *P. coelivaga*) [1*, homoplasious]; antennal toruli each with a single lateral antennifer [2]. **Male Terminalia:** Anterolateral apodemes of 9th sternite deflected ventrad of a pair of imaginary lines continued anteriorly from proximal ends of lateral costae [15*, unique]; 9th Gonocoxites with true superprocesses [24*, unique]; apex of mediuncus emarginate or bifid [32*, unique]; apodeme of adductor muscle of mediuncus inserting at base of terminal mediuncal cleft (secondarily displaced ventrally in *P. barnardi*) [36*, unique]. **Female Terminalia:** Suprastylar setae of 9th gonocoxite >50% cochleariform [54*, homoplasious]; spermatheca not bearing a pair of ventrolateral lobes [58].

**Distribution.**—Southeastern Asia (*Balmes*) and Australia (*Psychopsis* and 1 incertae sedis species).

**Included Taxa.**—*Balmes* (four species, including one undescribed), *Psychopsis* (12 species), and one incertae sedis species [see Appendix 1].

### Genus BALMES Navás, revised status
Figs. 6-11, 40

*Balmes* Navás, 1910:85 [Type species: *Balmes terissinus* Navás, 1910:85, by monotypy. Etymology: from the surname of Catalan philosopher Jaime Luciano Balmes [1810-1848], see Navás, 1910:85. Gender: Masculine (implied from the original combination *Balmes terissinus*).].—Navás, 1917 [taxonomy]; Kimmins, 1939 [taxonomy]; New, [1989a] [nomenclature].

**Nomenclatural Note.**—*Balmes* is here resurrected from synonymy with *Psychopsis*. Justification for this action is given below under the heading "Phylogenetic Analysis: Classification."

**Diagnosis.**—Cladistic analysis character numbers bracketed ([xx]), synapomorphies asterisked (*). **Head:** Vertex bearing 2 well-developed ocellar/cranial pulvinae [1]. **Wings:** Forewing without light brown transverse bars [4]; forewing costal gradate series absent or reduced (i.e., <6 crossveins) [6*, homoplasious]; hind wing without a dark distal macula [9]. **Male Terminalia:** 8th sternite without a posteromedian lobe [11]; 9th tergite without free posteroventral processes [12]; 9th sternite not narrow and parallel sided in ventral view [16], its apex shallowly emarginate or rounded [19]; 9th Gonocoxites: ventral costae absent or reduced to short thickenings [21*, homoplasious], dorsolateral sclerotized plates not flared laterally [22],
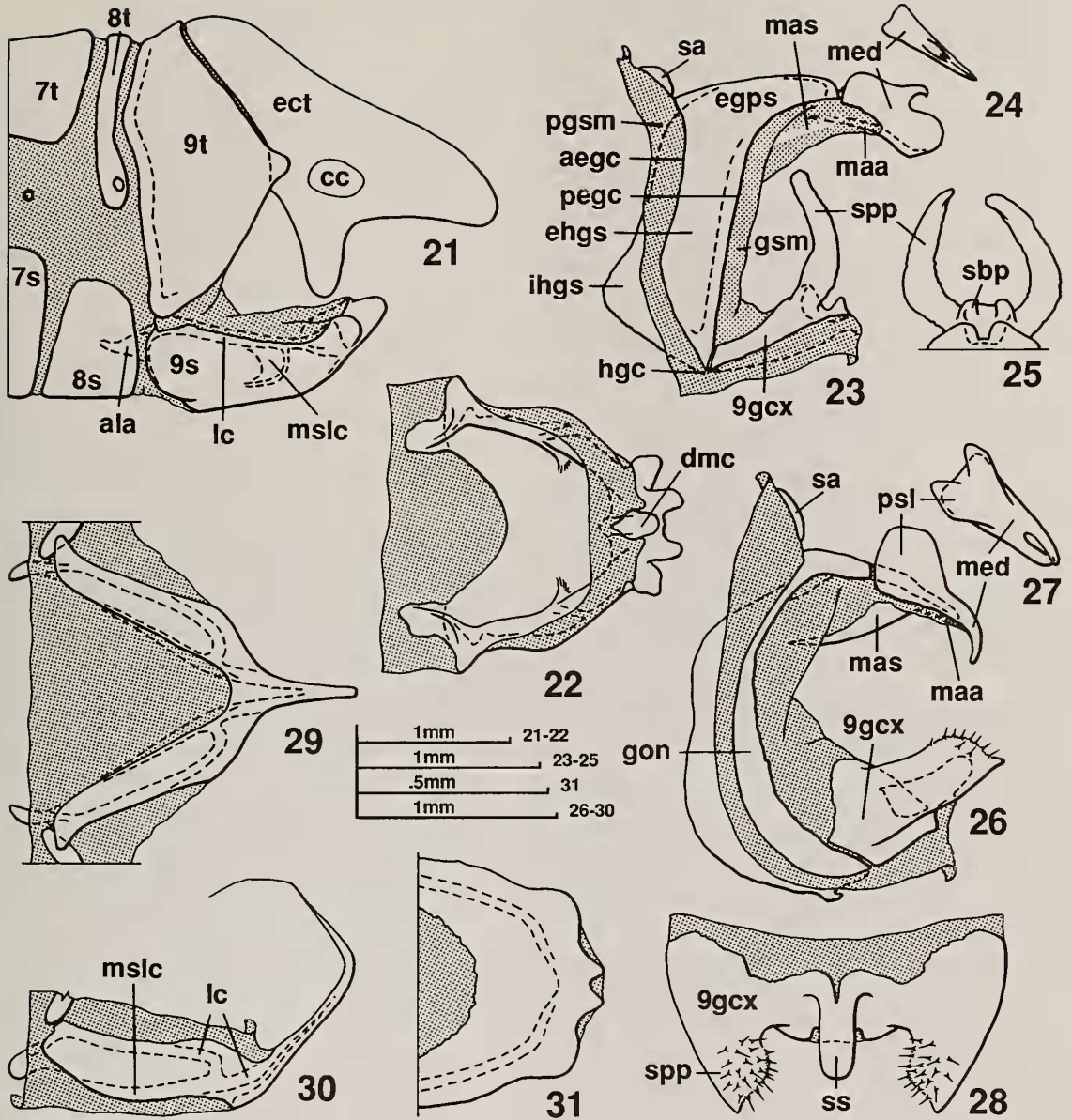
Figs. 21-31, *Psychopsis* species, males. 21-25, *P. barnardi*. 21, abdominal apex, lateral. 22, 9th sternite, dorsal. 23, gonarcus and 9th gonocoxites, lateral. 24, mediuncus, dorsal. 25, apices of 9th gonocoxites, posterior. 26-30, *P. illidgei*. 26, gonarcus and 9th gonocoxites, lateral. 27, mediuncus, dorsal. 28, 9th gonocoxites, dorsal. 29, 9th sternite, ventral. 30, same, lateral. 31, *P. coelivaga*, 9th sternite, ventral. Abbreviations: 7s, 8s, 9s, sternites; 7t, 8t, 9t, tergites; 9gcx, 9th gonocoxite; aegc, antextragonarcal commissure; ala, anterolateral apodeme; cc, cercal callus; dmc, dorsomedial cavity; ect, ectoproct; egps, extragonopons; ehgs, extrahemigonarcus; gon, gonarcus; gsm, gonosaccal membrane; hgc, hemigonarcal conjunction; ihgs, intrahemigonarcus; lc, lateral costa; maa, mediuncal adductor apodeme; mas, mediuncal accessory sclerite; med, mediuncus; mslc, mesal spur of lateral costa; pegc, postextragonarcal commissure; pgsm, paragonosaccal membrane; psl, parasagittal lobe; sa, subanale; sbp, subprocessus; spp, superprocessus; ss, sagittal spine.

superprocesses present but fused, represented by a transverse tumulus at the distal end of the conjoined gonocoxites [24*, unique]; mediuncus weakly decurved [33], not recurved [34]; gonosaccal membrane bearing spiculate lobes [39*, homoplasious]. **Female Terminalia**: Posterior margin of 7th sternite medially depressed and emarginate [40]; 7th and 8th sternites fused [43*, homoplasious]; 8th sternite narrow and transverse [44]; 9th Gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa [52], without a compact aggregation of setae borne adjacent to insertion of stylus [53], suprastylar setae >50% cochleariform [54]; bursa without lateral corniform diverticulae [57]; spermatheca lacking hollow ventrolateral lobes [58].

**Natural History and Immature Stages.**—No data.

**Distribution.**—Southeast Asia (southern China, Burma, Laos, Taiwan).

**Species.**—Four, including one undescribed [=bns1] (see Appendix 1; no recent authoritative species key exists). New's ([1989a]) treatment of *terissinus* as a junior synonym of *birmanus* appears to be faulty. I have examined males of three terminalically distinct *Balmes* species from mainland southeast Asia (i.e., excluding Taiwan); these are treated in Appendix 1 under the names *terissinus*, *birmanus*, and bns1. I have seen a long series of specimens (ca. 20 males, mostly in the USNM) that exhibit forewing maculation patterns closely matching Navás' original forewing illustration (1910:86, fig. 24) of *terissinus*. I have tentatively referred these specimens to *terissinus* based on their matching forewing maculations and their terminalic distinctness from specimens here attributed to *birmanus* and bns1, both of which lack the distinctly contrasting forewing maculae of *terissinus*. The specimens attributed here to *birmanus* closely correspond to New's ([1989a]:859) illustrations of the male terminalia of this species. The third species, here informally designated bns1, is clearly distinct terminalically from both *terissinus* and *birmanus*. Particularly diagnostic is the sagittal process arising from the distally fused male gonocoxites [character 26] in this species. It is at least possible that bns1 represents the unknown male of *formosa*; however, it is also possible that it represents an entirely new species. The discovery of still other *Balmes* species in the poorly collected areas of southeast Asia cannot be ruled out. A comprehensive review of material from this area is

currently needed to definitively resolve these issues.

## Genus **PSYCHOPSIS** Newman
Figs. 21-38, 42, 48-52

*Psychopsis* Newman, 1842:415 [Type species: *Psychopsis mimica* Newman, 1842:415, by monotypy. Etymology: unexplained, probably Psych- (from Gr. *psyche*, butterfly) + -opsis (from Gr. *opsis*, appearance). Gender: Feminine.].—Navás, 1917 [taxonomy]; Tillyard, [1919a] [taxonomy]; Krüger, 1922 [taxonomy]; Kimmins, 1939 [taxonomy]; New, [1989a] [taxonomy].

*Artiopteryx* Guérin-Ménéville, [1844]:389 [Type species: *Artiopteryx elegans* Guérin-Ménéville, [1844]:389, by monotypy. Etymology: unexplained, probably, Artio- (from Gr. *arteria*, artery) + -pteryx (from Gr. *pteryx* [fem.], wing). Gender: Feminine.].—Erichson, 1847 [note]; Hagen, 1866 [synonymy, as *Arteriopteryx* (sic)].

*Arteriopteryx* [sic] Hagen, 1866:380 [An incorrect subsequent spelling of *Artiopteryx*. Although probably intended as an emendation of *Artiopteryx* (see etymology above), Hagen's spelling does not meet the Code's emendation requirements because the original spelling was not explicitly cited, Art. 33b(i).].—Oswald & Penny, 1991 [nomenclature].

*Magallanes* Navás, 1912b:197 [Type species: *Psychopsis insolens* McLachlan, 1863:114, by original designation. Etymology: From the surname of Portuguese navigator Fernao de Magalhaes (=Ferdinand Magellan) [1480?-1521], see Navás, 1912b:197. Gender: No originally attributed or implied gender, here considered masculine, Art. 30.].—Navás, 1917 [taxonomy]; Tillyard, [1919a] [synonymy]; Kimmins, 1939 [taxonomy]; New, [1989a] [synonymy].

*Wernzia* Navás, 1912b:195 [Type species: *Hemerobius coelivagus* Walker, 1853:279, by original designation. Etymology: from the surname of M. R. P. Francisco Wernz, General de la Compañía de Jesús, see Navás, 1912b:195 and Navás, 1917:194. Gender: Feminine (implied from the original combination *Wernzia caelivaga* [sic]).].—Navás, 1917 [taxonomy]; Tillyard, [1919a] [synonymy]; Kimmins, 1939 [taxonomy]; New, [1989a] [synonymy].

*Megapsychops* Tillyard, [1919a]:771 [Type species: *Psychopsis illidgei* Froggatt, 1903:455, by original designation. Etymology: unexplained, probably Mega- (from Gr. *megas*, large) + -psych- (from Gr. *psyche*, butterfly) + -ops (from Gr. *ops* [fem.], countenance). Gender: Masculine, Art. 30a(ii).].—Kimmins, 1939 [taxonomy]; New, [1989a] [taxonomy]. NEW SYNONYM

*Psychopsella* Tillyard, [1919a]:780 [Type species: *Psychopsella gallardi* Tillyard, [1919a]:780, by original designation. Etymology: unexplained, probably

Psych- (from Gr. *psyche*, butterfly) + -ops- (from Gr. *ops*, countenance) + -ella (from L. diminutive suffix *-ella*). Gender: Feminine, Art. 30b.].—Kimmins, 1939 [synonymy].

*Orientichopsis* Kuwayama, 1927:125 [As a subgenus of *Psychopsis*. Type species: *Psychopsis* (*Orientichopsis*) *formosa* Kuwayama, 1927:123, by original designation. Etymology: unexplained, probably Orienti- (from L. *orientis*, east) + -chopsis (from the generic name [*Psy*]*chopsis* [fem.]). Gender: Feminine.].— Kimmins, 1939 [synonymy].

**Nomenclatural Note.**—*Megapsychops* is here reduced to a junior synonym of *Psychopsis*. Justification for this action is given below under the heading "Phylogenetic Analysis: Classification."

**Diagnosis.**—Cladistic analysis character numbers bracketed ([xx]), synapomorphies asterisked (*). **Head**: Vertex bearing 2 well-developed ocellar/cranial pulvinae, vestigial remnants of a third (ventromedial) pulvinus sometimes present (all pulvinae lost in *coelivaga*) [1]. **Wings**: Forewing without light brown transverse bars [4]; forewing costal gradate series well developed [6]; hind wing with a dark distal macula [9*, unique], but variable in position relative to the "anastomosis." **Male Terminalia**: 8th sternite without a posteromedian lobe [11]; 9th tergite without free posteroventral processes [12]; 9th sternite not narrow and parallel sided in ventral view [16], its apex of variable form [19]; 9th Gonocoxites: ventral costae generally long and prominent (reduced in *gracilis* and *illidgei*) [21], dorsolateral sclerotized plates not flared laterally when present [22], superprocesses present, their conformations variable [24]; mediuncus linear or weakly decurved [33], not recurved [34]; gonosaccal membrane without spiculate lobes (except in *insolens*) [39]. **Female Terminalia**: Posterior margin of 7th sternite medially depressed and emarginate [40]; 7th and 8th sternites not fused (except in *illidgei*) [43]; 8th sternite narrow and transverse to broadly triangular or trapezoidal [44]; 9th Gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa [52], with a compact aggregation of setae borne adjacent to insertion of stylus [53*, unique], suprastylar setae >50% cochleariform [54]; bursa without lateral corniform diverticulae [57]; spermatheca lacking hollow ventrolateral lobes [58].

**Natural History and Immature Stages.**—Larvae of *elegans*, *mimica*, and *coelivaga* have been mentioned in the literature (Froggatt, 1902 [*elegans* (as *mimica*), 1907 [*elegans*]; Tillyard, [1919b] [*elegans*,

*coelivaga*]; Gallard, 1914 [*elegans* (as *newmani*)], 1922 [*mimica*], 1923 [*mimica*]; Withycombe, [1925] [*elegans*]; MacLeod, 1964 [*elegans*]). The most detailed life history account is that of Tillyard ([1919b]) for *elegans*. Larvae of *elegans* and *coelivaga* were field collected under the bark of healthy, rough-barked, Myrtaceous trees (primarily *Eucalyptus* species). Larvae appear to aggregate around sap flows where they are presumed to feed on small arthropods attracted to the exudates. Two-year life histories have been documented for both *elegans* (see Tillyard, [1919b]) and *mimica* (see Gallard, 1923). MacLeod (1964) presented a detailed treatment of the larval cephalic morphology of *elegans*.

**Distribution.**—Australia, reported from all states except Tasmania. Most species, however, are restricted to or primarily distributed within the tropical to mesic temperate mountainous areas of eastern Australia. Records from western, particularly northwestern, Australia are scarce (collection bias?).

**Species.**—Twelve, plus one incerta sedis species which may belong here (see Appendix 1; Key: New, [1989a]: 843-845).

## FUNCTIONAL MORPHOLOGY OF MALE AND FEMALE TERMINALIA

The functional morphology of male and female terminalic structures and the mechanics of copulation are poorly known for most neuropterous taxa, and no such information has been available for the family Psychopsidae. Research conducted for this work included detailed morphological examinations of both the male and female terminalia for nearly all species studied (five species were available in only one sex). The primary objective of these morphological studies was the individualization of characters and character states for the inference of phylogenetic relationships among extant psychopsids. The studies, however, also revealed something unexpected —the presence of a distinctive, and previously unnoticed, copulatory apparatus in the sclerotized components of both the male and female terminalia.

In the sections below I have drawn together numerous scattered observations on individual male and female terminalic components, and placed them together in a common context to provide a broad overview of psychopsid copulation and oviposition. This discussion is divided into two parts. First, I present a relatively detailed survey of the psychopsid male and female terminalia them-

selves. This section focuses on the morphology of
the sclerites of the terminalic complex, including
their modifications, fusions, articulations,
apodemes, costae, and connecting membranes.
Second, I discuss the mechanics of copulation and
oviposition based on inferences derived from the
morphological observations. The information and
hypotheses presented here are based on observa-
tions of macerated and stained terminalic prepara-
tions from dried specimens.

## MORPHOLOGICAL OBSERVATIONS

### MALES

The sclerotized components of the male
terminalia (Figs. 1, 3) can be divided into two
systems: (1) an outer system comprised of the 8th
tergite and sternite [8t, 8s], 9th tergite and sternite
[9t, 9s], ectoprocts [ect] (=10th [+?11th] hemitergites
+?cerci), and subanale [sa] (=?10th sternite rem-
nant); and (2) an inner system comprised of the
gonarcus [gon] (dorsomedially fused volsellae,
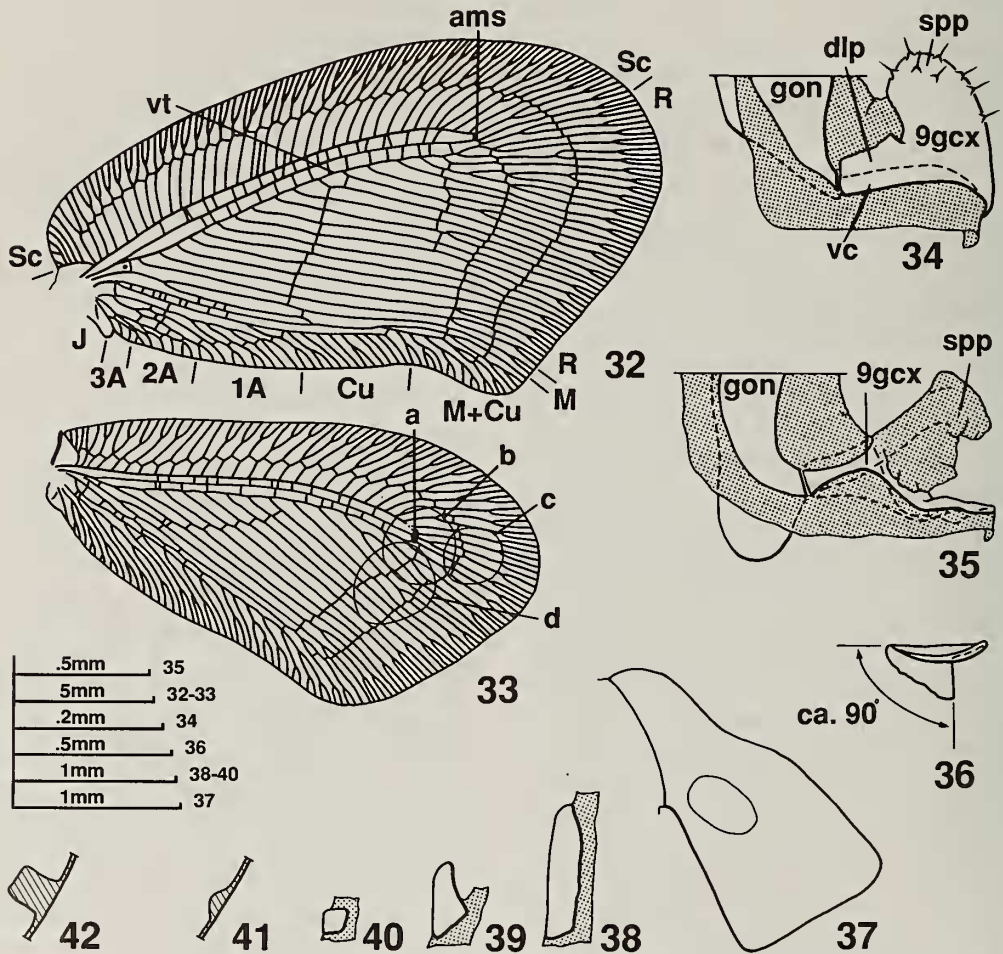


Figs. 32-42. 32-33, *Psychopsis barnardi*. 32, forewing. 33, hind wing. 34-35, Male 9th gonocoxites, lateral. 34, *P. coelivaga*. 35, *P. elegans*. 36, *P. barnardi*, hypandrium internum, lateral. 37, *P. elegans*, male ectoproct, lateral. 38-40, Forewing humeral plates, dorsal. 38, *P. barnardi*. 39, *Silveira marshalli*, 40, *Balmes birmanus*. 41-42, lateral costae of male 9th sternite, diagrammatic cross-sections. 41, *Silveira marshalli*. 42, *Psychopsis barnardi*. Abbreviations associated with the illustrations: **1A, 2A, 3A**, anal veins; **9gcx**, 9th gonocoxite; **ams**, anastomosis; **Cu**, cubitus; **dlp**, dorsolateral plate; **gon**, gonarcus; **J**, jugal vein; **M**, media; **M+Cu**, media + cubitus; **R**, radius; **Sc**, subcosta; **spp**, superprocessus; **vc**, ventral costa; **vt**, vena triplica.

sensu Adams, 1969), mediuncus [med] (a gonarcus fragment), mediuncal accessory sclerites [mas] (novel psychopsid sclerites), 9th Gonocoxites [9gcx] (sensu Adams, ="parameres" of many other authors), and hypandrium internum (a small sclerite associated with apex of eversible gonosaccal membrane).

**Outer System (Male).**—**8th Tergite**, free, hemiannular, very narrow, ventrolateral extremities enclosing spiracles of 8th somite in most species. **9th Tergite**, ± hemiannular; narrowed (particularly dorsally); antecosta prominent (at least ventrally); lateral extremities extended ventrally well below level of pleural membrane, their ventral apices articulating with anterolateral angles of 9th sternite. **Ectoprocts**, free, completely separated dorsally, membranously associated with posterior margin of 9th tergite; antecosta prominent to lacking; generally singly lobed posteriorly, bilobed in a few species (i.e., *Psychopsis illidgei* and *barnardi*, and *Silveira occultus*); cercal callus present, bearing trichobothria. **8th Sternite**, free, hemiannular, slightly narrowed dorsally, but largely unmodified in most species, with a small posteromedian bulge in some zygophlebiines. **9th Sternite**, free, anterolateral angles articulating with 9th tergite, each articulation braced by a lateral longitudinal costa, lateral costae occasionally with mesal spurs, but always continued internally as short apodemes beyond their articulations with 9th tergite; ventral surface of sclerite between lateral costae largely unsclerotized in many species; apical configurations highly varied, sometimes bearing prominent distal lobes, often sagittally emarginate; in a few *Psychopsis* species bearing a heavily-walled, sagittal pit, dorsodistally (Fig. 22, dmc); **Subanale**, always present, a small, setose, sclerite lying medially in the paragonosaccal membrane between the gonarcus and anus.

The 8th and 9th tergites, 8th sternite, and subanale appear to be largely immobile sclerites, disregarding the extension and compression motions of the abdomen. The ectoprocts articulate loosely on the ipsilateral posterior margins of the 9th tergite; and their motions are principally lateral/medial. The anterolateral angles of the 9th sternite articulate dicondylically with the ventrally elongate lateral extremities of the 9th tergite, which restricts 9th sternite motion to a dorsal/ventral arc around this articulation. The ectoprocts and 9th sternite, respectively, enclose the abdominal apex posterodorsally and posteroventrally, providing

protection for the sclerites of the inner system. In some taxa the 9th sternite apex is modified to receive the apical portion of the mediuncus. For example, the mediuncal apex in several *Silveira* species has been observed resting in the apical emargination of the 9th sternite; and, the dorsomedial pit located near the apex of the 9th sternite in some *Psychopsis* species (e.g., *elegans*, *mimica*, and *barnardi*) appears to be a mediuncal receptacle.

**Inner System (Male).**—**Gonarcus** (Fig. 23), a well-developed, upright, sclerotized arch; comprised of an externally exposed *extragonarcus* (the *extrahemigonarcus* [ehgs] laterally, *extragonopons* [egps] dorsally), and an internal, apodemal, *intragonarcus* (the *intrahemigonarcus* [ihgs] laterally, *intragonopons* [absent or poorly developed in most psychopsids] dorsally); suspended between the ectoprocts by the *paragonosaccal membrane* [pgsm], which meets the gonarcus along a line, the *antextragonarcal commissure* [aegc], which separates the extra- and intragonarcus; posterior margin of extragonarcus confluent with *gonosaccal membrane* [gsm] along *postextragonarcal commissure* [pegc]; ant- and postextragonarcal commissures meeting (or nearly so) at a pair of points, the *hemigonarcal conjunctions* [hgc], at posteroventral angles of *hemigonarcus*; extragonopons generally prolonged posteriorly; extrahemigonarcus with a prominent posterior process (Fig. 13, ehgp) in *Zygophlebius zebra* and *leoninus*; intragonarcus variously developed, intragonopons frequently absent; mediuncus articulated along posterior margin of the extragonopons; paired 9th gonocoxites associated with posteroventral angles of hemigonarcus.

Although the gonarcus clearly serves as a rigid framework upon which the mediuncus and 9th gonocoxites articulate, the range of motion of this linked complex of three sclerites (taken as a unit) within the abdominal apex is difficult to ascertain. Based on its loose membranous association with the sclerites of the outer system, it would appear to be capable of a considerable range of motion during copulation, particularly protrusion posteriorly.

**Mediuncus** (Figs. 13-15, med), a small, secondarily disassociated, posteromedian fragment of the extragonarcus, now articulated with the posterior margin of the extragonopons at a transversely oriented joint; apex simple (Zygophlebiinae) or cleft/emarginate (Psychopsinae); bearing internally a discrete apodeme upon which the mediuncal adductor inserts.

Tjeder (1960) and New ([1989a]) used the term *arcessus* for this structure. I adopt "mediuncus" because it is consistent with Tjeder's original (1931:3, fig. 1) use of mediuncus for the dorsodistal portion of the "10th sternit [sic]" (i.e., gonarcus), and thus clearly connotes the homology of the articulated sclerite in psychopsids with the apex of the extragonarcus. The presence of an articulated mediuncus in psychopsids may or may not be homologous with one or more of the similar states found in other neuropterous families. Given the wide but sporadic distribution of both articulated and disarticulated mediunci within the Neuroptera, it is almost certain that functionally similar transverse articulations have developed in numerous neuropterous lineages independently. Because the articulation is ubiquitous, and therefore interpreted as plesiomorphic, within the Psychopsidae, its possible extrafamilial homologies have not been investigated in detail here. In psychopsids the mediuncus generally articulates with the extragonopons by means of a pair of sclerotized parasagittal lobes (sometimes poorly developed) borne on the proximodorsal margin of the mediuncus. This articulation restricts mediuncal motion to a vertical arc around the transverse posterior margin of the extragonopons.

**Mediuncal Accessory Sclerites** (Fig. 14, mas), a bilaterally symmetrical pair of narrowly elongate and weakly sclerotized straps originating in the gonosaccal membrane beneath the extragonopons and inserting posteriorly on (or at least closely associated with) the lateral or ventrolateral surfaces of the mediuncus. These structures appear to be a psychopsid novelty. Although their function is uncertain, their association with the mediuncus suggests that they may play a role in mediuncal adduction.

**9th Gonocoxites** (Fig. 23, 9gcx), a pair of partially setose, bilaterally symmetrical sclerites associated with the posteroventral angles of the hemigonarcus, and which are clearly fused sagittally (except in *Psychopsis coelivaga*, where the gonocoxite apices are closely associated, but not fused) to form an arcuate ventral bridge between the hemigonarcus; variously lobed distomedially, superprocesses present in all psychopsine species, absent in zygophlebiine species; each gonocoxite usually bears internally a ventrolongitudinal costa, sometimes also with distoventral apodemes. In nearly all psychopsid species, the motion of the 9th gonocoxites is a dorsal-ventral arc around their

more or less dicondylic articulation with the posteroventral angles of the hemigonarcus. The only exception I have noted to this condition is found in *Psychopsis illidgei* (Fig. 26), where the gonocoxites overlie, and are joined for a considerable distance to, the posteroventral margins of the extrahemigonarcus. In this species, the 9th gonocoxites may be essentially fixed in position, although a clear suture separating the two sclerites is still present.

**Hypandrium Internum** (Fig. 36), a small sclerite of standard neuropterous form, i.e., triangular dorsal view, with a depressed median longitudinal keel and revolute lateral margins. This sclerite is associated with the apex of an eversible, membranous gonosaccus and may serve as an insertion site for gonosaccal adductor muscles.

FEMALES

Female terminalic structures (Fig. 43) can be divided into two systems: (1) an outer system of sclerites comprised of the 7th sternite [7s], 8th tergite [8t] and sternite [8s; =praegenitale, sensu Tjeder], 9th tergite [9t], subgenitale [sg], 9th gonocoxites [9gcx, sensu Adams; =gonapophyses laterales, sensu Tjeder), 9th gonocoxite styli [sty], ectoprocts [ect] (=10th [+?11th] hemitergites [+?cerci]), subanale (Tjeder, 1960:179, fig. 358, sap; =?10th sternite remnant), and postgenitalia (Tjeder, 1960:179, fig. 359, pop); and (2) an inner system of principally membranous components comprised of the posterior abdominal chamber [pacm; ="genital chamber" in part, sensu Tjeder], oviducts, bursa [Fig. 47, bur; ="spermatheca" in part, sensu Tjeder], and bursal appendages, i.e., the colleterial gland, colleterial accessory gland, bursal accessory gland(s) [Fig. 47, bag; = "glandulae accessoriae," sensu Tjeder], spermatheca [Fig. 46; ="spermatheca" in part, sensu Tjeder], and fertilization canal [Fig. 46, fzc].

**Notes on Terminology and Homology.**—Tjeder (1960) treated the ultimate and penultimate ventral sclerites of the female abdomen anterior to the ovipore under the names subgenitale and praegenitale. I interpret Tjeder's praegenitale as the female 8th sternite. The setiferousness of this sclerite (except in *Silveira*, where the loss of setae apparently facilitates insertion of the male 9th gonocoxites under the posterior margin of the female 7th sternite during copulation), together with its location immediately behind the 7th sternite

Figs. 43-52. 43-47, *Zygophlebius* new species (=zns1), female. 43, abdominal apex, lateral (membranous posterior abdominal chamber artificially everted to show its extent and proximal association with 9th tergite). 44-45, 7th and 8th sternites showing inflated copulatory fovea. 44, ventral. 45, dorsal. 46, spermatheca, lateral. 47, portion of bursa showing corniform diverticula and associated bursal accessory gland, dorsal. 48-50, *P. barnardi*, female. 48, spermatheca, ventral. 49, 7th and 8th sternites showing configuration of copulatory fovea, ventral. 50, same, with sternites in sagittal section and with male mediuncus/gonarcus/9th gonocoxite complex shown in its presumed copulatory position. 51-52. *P. elegans*, female. 51. 7th and 8th sternites showing configuration of copulatory fovea, ventral. 52, same, sternites in sagittal section. Abbreviations associated with the illustrations: **7s, 8s**, sternites; **7t, 8t, 9t**, tergites; **9gcx**, 9th gonocoxite; **ala**, anterolateral apodeme; **bag**, bursal accessory gland; **bur**, bursa; **cc**, cercal callus; **cd**, corniform diverticula; **cf**, copulatory fovea; **da**, distal apodeme; **ect**, ectoproct; **fzc**, fertilization canal; **gon**, gonarcus; **lap**, lateral apodemal plate; **med**, mediuncus; **mvc**, midventral carina; **pacm**, posterior abdominal chamber membrane; **sg**, subgenitale; **sty**, stylus; **vll**, ventrolateral lobe.

and frequently transverse orientation corroborate its homology with the 8th sternite.

The homology of Tjeder's subgenitale is less certain. Its position between the 8th sternite and ovipore can be interpreted as (1) a pair of fused 8th gonocoxites [+?8th gonapophyses], (2) a 9th sternite, or (3) a novel secondarily developed sclerite. Since information available on this sclerite is currently inconclusive as to its homology, I have retained for it Tjeder's neutral term subgenitale. In psychopsids, the subgenitale is always small, asetose, and bears a pair of protrudent posterolateral lobes that insert into a pair of shallow depressions, one borne on the membranous anteromedian face of each female 9th gonocoxite. The weakly sclerotized portions of these depressions were designated postgenitalia by Tjeder (1960). They were interpreted as 9th gonapophyses by MacLeod and Adams ([1968]:248) in berothids, but are here regarded as simple secondary sclerotizations of the inner walls of the 9th gonocoxites, for which the name postgenitalia is retained. This system, i.e., a terminally bilobed subgenitale mating with a pair of impressed and weakly sclerotized "postgenitalia," is a common feature in many neuropterous families (e.g., Chrysopidae, Hemerobiidae, Psychopsidae, Nymphidae, Polystoechotidae). The system may have evolved as a mechanism to seal the posteroventral aspect of the abdomen—by linking the contralateral 9th gonocoxites, thus concealing the ovipore—and/or as a means of directing ova emerging from the ovipore into the sagittal canal between the female 9th gonocoxites (Bitsch, 1984:36). The wide distribution of this system within the Neuroptera suggests that it is either of considerable antiquity or has evolved parallelly in numerous lineages.

I adopt here the homologization by MacLeod and Adams ([1968]:248) of Tjeder's "gonapophyses laterales" with the female 9th gonocoxites; the later term is used here.

The exocrine gland appendages of the neuropterous bursa have yet to be adequately surveyed in a comparative manner across the families of the Neuropterida (Kristensen, 1981; = Neuroptera + Megaloptera + Raphidioptera). Thus, homologies among these glands must be regarded as tentative. This has lead to several terminological uncertainties. A particular problem is the simple appellation "bursal gland(s)," which has several distinct usages. This name has been used for apparently non-homologous paired and unpaired glands and might

also be applied, collectively, to all glands opening on or near the bursa. In the interest of developing a more precise glandular terminology, I recommend that the simple, unmodified, phrase "bursal gland(s)" be reserved for the collective sense above and that other terms or modified phrases be adopted for presumably homologous glands or gland pairs. Accordingly, I use the designation bursal accessory glands (=glandulae accessoriae of Tjeder, 1960:203, fig. 448) for the plesiomorphic pair of glands inserted distally on the bursa in psychopsids. Similar, possibly homologous, paired glands are found in many other neuropterid families (e.g., Principi, 1949:332, fig. 14, "glandole della borsa copulatrice" [Chrysopidae]; Monserrat, 1990:71, figs. 11-12, 14 [Hemerobiidae]; Adams, 1969:7, fig. 6, "spermatheca" [Osmylidae]; Quartey and Kumar, 1973:94, fig. 8, "accessory glands" [Ascalaphidae]; Oswald, unpublished data, *Nymphes* [Nymphidae], *Agulla* [Raphidiidae], *Halter* [Nemopteridae], *Polystoechotes* [Polystoechotidae]). An additional, unpaired, gland is present in at least some raphidiids (e.g., *Agulla*) and osmylids (e.g., *Kempynus*).

**Outer System (Female).**—**8th Tergite** (Fig. 43), hemiannular, very narrow dorsally, wider ventrally; enclosing spiracles of 8th somite; posteroventral margins solidly fused to 9th tergite; posterodorsal fusion less complete, approximate path of 8t/9t suture generally well marked by 9th tergite antecosta. **9th Tergite**, narrow dorsally, greatly expanded posteroventrally; antecosta dorsal to spiracles of 8th somite produced as a pair of short, broad, apodemes; posteroventral margins pilose and inwardly revolute. **Ectoprocts**, subtriangular; apices attenuate, inwardly revolute, and pilose; anterior margins partially fused to 9th tergite, but the intervening suture lines are generally discernable; cercal callus present, bearing trichobothria. **Subanale**, prominent; setose. **7th Sternite**, ± hemiannular; posterior margin generally emarginate or undulate; posteromedial surface modified, generally as a distinct depression; antecosta generally prominent. **8th Sternite**, highly and variously modified in all species, narrow and transverse (e.g., *Silveira, Balmes*), to small and globular (e.g., *Cabralis, Zygophlebius*), or secondarily enlarged and triangular/trapezoidal (e.g., many *Psychopsis*); free or fused to posterior margin of 7th sternite; anteromedian surface sometimes depressed. **Subgenitale**, vestigial; a small, asetose, plate bearing a pair of small lateral protuberances. **9th Gonocoxites**, present; spathulate; each bears

(1) a dorsolongitudinal costa, (2) a subapical stylus, and (3) an apical-subapical aggregation of elongate, spathulate, setae. **9th Gonocoxite Stylus**, present; arising subapically from the ventral surface of the 9th gonocoxites; always bears a ventral field of highly modified "digging" setae. **Postgenitalia**, present; a pair of small, weakly sclerotized, invaginations located at the proximal ends of the membranous mesal walls of the 9th gonocoxites.

**Inner System (Female).**—**Posterior Abdominal Chamber**, present, a large internal space bounded by a membranous sac that fills the hollow created by the fused 8th and 9th tergites and ectoprocts; opens posterior to bursal opening and 9th gonocoxite insertions between pilose posteroventral margins of 9th tergite; lacks inserted exocrine glands. **Bursa**, a large membranous sac opening ventrally behind subgenitale and between bases of 9th gonocoxites; walls continuous ventrally with spermatheca; frequently containing amorphous spermatophore remnants; colleterial and colleterial accessory glands present, opening through membrane joining contralateral 9th gonocoxites, which is continuous with dorsal wall of bursa; one pair (2 pairs in some *Zygophlebius*) of bursal accessory glands present, each gland opening on dorsodistal surface of bursa through a separate duct (a single duct in *Balmes birmanus*; apparent points of insertion may vary depending upon degree of inflation of bursa). **Spermatheca**, a well-sclerotized, longitudinally oriented, structure attached to ventromedial aspect of bursa; slit-entry type, with narrow dorsal slit effectively dividing spermathecal (proximal) portion of insemination/fertilization canal from main bursal chamber; sometimes bearing prominent apodemes (e.g., some *Psychopsis* species, Fig. 48, lap) or lobes (i.e., Zygophlebiinae, Fig. 46, vll). **Insemination/Fertilization Canal**, proximal portion passing through spermatheca, constricted at proximal end of spermatheca and continued toward common oviduct as a thin duct.

HYPOTHESIZED MECHANICS OF
COPULATION AND OVIPOSITION

COPULATION

**Overview.**—Copulation is the coupling of male and female terminalia preparatory to sperm transfer. In psychopsids, stable coupling is presumed to be accomplished by active confinement of the female 8th sternite between the opposable mediuncus and 9th gonocoxites of the male. The principal actions in the hypothesized copulatory sequence are listed in temporal order below. The numbered actions correspond to identically numbered sections given under the succeeding heading, "Evidence," where morphological evidence supporting each action is presented.

**Copulatory Sequence.**—(1) Copulation occurs venter to venter with the abdominal apices oriented in opposite directions. (2) The male mediuncus is inserted into the female copulatory fovea. Adduction of the mediuncus, by flexion of the mediuncal adductor muscle, partially links the abdomens together by rotating the apex of the mediuncus internally under the female 8th sternite or by solidifying its position within the fovea. While adducted, the proximodorsal surface of the mediuncus lies adjacent or adpressed to the posteromedian surface of the female 7th sternite. (3) Concurrent adduction of the male 9th gonocoxites, whose distal surfaces catch on or under the posterior margin(s) of the female 7th or 8th (or both) sternite(s), opposes the action of the mediuncus. The combined motions of the male mediuncus and 9th gonocoxites lock the male and female terminalia together by trapping the female 8th sternite between the mediuncus, anteriorly, and the 9th gonocoxites, posteriorly [except in *Silveira*, see Taxonomic Differences below]. (4) Following this linkage, access to the external opening of the female bursa—at rest concealed by the overlying 9th gonocoxites and ventrally extended lateral surfaces of the 9th tergite—is probably provided by lateral separation of the free, but sagittally adpressed, female 9th gonocoxites. This separation is most likely accomplished by the imposition between them of the apex of the male 9th sternite. (5) With the female 9th gonocoxites spread and the bursal opening exposed, the male gonosaccus is everted directly into the bursa, where the spermatophore is deposited.

**Evidence.**—(1) This orientation is the standard copulatory position in neuropterid insects (e.g., Megaloptera: Elliott, 1977:33, fig. 13 [Sialidae]; Neuroptera: Johnson and Morrison, [1980]:396 [Coniopterygidae]; Principi, 1949:353, fig. 29 [Chrysopidae]; Hennig, 1990:194, fig. 5 [Myrmeleontidae]), and is corroborated in psychopsids by the orientations and alignments of individual male and female terminalic components.

(2) The principle evidence supporting insertion

of the male mediuncus into the ventromedian fovea between female sternites 7 and 8 during copulation is the close correlation between male mediuncal shapes and female foveal configurations (including modifications to the adjacent portions of the female 7th and 8th sternites). This evidence seems incontrovertible. Summaries of the correspondence between the morphologies of the male mediuncus and female copulatory fovea and sternites in each psychopsid genus are given below.

*Silveira*. The copulatory fovea is a narrow chamber into which the slender male mediuncal apex is inserted. Adduction of the mediuncus rotates the mediuncus under the narrow, transverse, straplike 8th sternite, and presses the proximodorsal surface of the mediuncus against the posteromedian surface of the female 7th sternite. In *Silveira rufus*, *occultus*, and *marshalli* the dorsal surface of the male mediuncus bears a pair of elevated proximolateral lobes. In females of these species the posteromedian depression of the 7th sternite is cordate, comprised of a pair of lateral depressions (which receive the mediuncal lobes) divided by a short anteromedian ridge (which receives the depression between the mediuncal lobes). In *jordani*, the male lacks dorsolateral mediuncal lobes, and the posteromedian depression of the female 7th sternite is simple, not cordate.

*Cabralis*. In both species the copulatory fovea is a posteriorly arched invagination that precisely mirrors the shape of the apically decurved male mediuncus. The female 8th sternite is a small rounded sclerite which forms an external reinforcing cap over the apex of the fovea. Except for its deep posteromedial emargination, which facilitates insertion of the large male mediuncus into the copulatory fovea, the posteromedian surface of the female 7th sternite is little modified.

*Zygophlebius*. The copulatory fovea in *zebra* and *leoninus* is a shallow pit bearing a narrow appendix into which the mediuncal apex inserts. In zns1 the fovea forms an inflated spheroid (also bearing an appendix). The shape in the latter species correlates with, and is likely a modification to accommodate, the distolateral setal tufts of the male mediuncus, which are present only in this species. The mediunci of all three species are recurved, and the degree of recurvature is positively correlated with the developmental state of the sagittal cusp on the posterior margin of the female 7th sternite (i.e., the larger the cusp the more recurved the mediuncus).

*Balmes*. In this genus the copulatory fovea is a shallow cavity protruded for a short distance under the anteromedian margin of the transverse 8th sternite. The fovea accommodates only the slightly curved apices of the male mediuncus.

*Psychopsis*. Copulatory foveae in this genus exhibit considerable interspecific variation, and include significant modifications to the female 7th and 8th sternites in most species. Mediuncus/(fovea+sternite) correspondence is most highly developed in the *illidgei* and *gracilis* species groups. For example: [1] in *illidgei*, the proximodorsal surface of the mediuncus bears a pair of erect lateral blades which fit into a symmetrical depression on the posteromedian surface of the female 7th sternite, and [2] in *barnardi* (Fig. 50), the enlarged (apomorphic) distoventral lobe of the mediuncus fits precisely into a deep, rounded, depression on the anteromedian face of the 8th sternite; sagittally, the anterior margin of this pit slightly overlaps the posterior margin of a smaller depression on the posteromedian surface of the 7th sternite; the emarginate distal surface of the plesiomorphic portion of the mediuncus (i.e., the small "hook" on the dorsal mediuncal surface) fits into the 7th sternite depression, with the plesiomorphic mediuncal apex catching on the overlapped 8th sternite margin; the mediuncus/(fovea+sternite) correlation in this species is especially striking.

(3) An active copulatory role for the male 9th gonocoxites is suggested by several aspects of their general morphology: [1] the presence of a ventral costa, which provides both stiffening for the narrow sclerites and reinforced sites for muscle insertion, [2] the presence of setae, suggesting a sensory role for these sclerites, and [3] the diversity of apical lobes on these sclerites. Given the position of their articulation with the gonarcus and their location ventral to the mediuncus, the most probable functional role of the 9th gonocoxites is to oppose the adduction of the mediuncus. This role is strongly supported by the automatic positioning of the 9th gonocoxites behind the posterior margins of the female 7th and 8th sternites when the mediuncus is inserted into the copulatory fovea. The copulatory positioning of the male 9th gonocoxites is discussed further under Taxonomic Differences below.

(4) At rest, the opening to the female bursa is concealed by the ventrally prolonged 9th tergites and the bases of the female 9th gonocoxites. Access to the bursal opening might be accomplished by either the posterior withdrawal of the 9th tergite/

gonocoxite complex or by lateral separation of the loosely adpressed gonocoxites. The latter mechanism seems simpler and is probably actually employed. Although spreading of the female 9th gonocoxites may be entirely under the voluntary control of the female, a number of morphological observations suggest that the male 9th sternite is structurally capable and positionally available to spread the female 9th gonocoxites after the male gonarcus/mediuncus/9th gonocoxite complex has firmly clasped the female.

First, it must be noted that the male 9th sternite articulates proximolaterally with the ventrolateral angles of the male 9th tergite. Distal to these points of articulation, the lateral margins of the 9th sternite bear strengthening longitudinal costae, which are also produced internally as a pair of short apodemes. The presence on the 9th tergite of well-sclerotized apodemes and articulations reinforced by thickened costae suggests that the motions of the 9th sternite are under active muscular control, and that abduction of the 9th sternite could exert significant pressure. Second, with the mediuncus and male 9th gonocoxites firmly grasping the female 8th sternite the ventral surface of the male 9th sternite lies directly against, or immediately adjacent to, the proximal ends of the female gonocoxites. This confirms that the 9th sternite, in copulatory position, occupies a position suitable to exert posterior pressure on the female 9th tergite and/or gonocoxites. Furthermore, the tightly linked male and female terminalia provide a solid foundation from which to exert such pressure. Third, since the adducted male 9th sternite closes the distoventral surface of the male abdomen, this sternite must be abducted at some time during copulation to allow eversion of the male gonosaccus. Fourth, in some taxa (e.g., Z. *leoninus* and *Silveira* species) the male 9th sternite appears longitudinally folded. One effect of such a fold could be to narrow the sternite along its midline, which could be an adaptation for easier penetration between the female 9th gonocoxites.

The alternative mechanism proposed for uncovering the opening to the bursa, i.e., posterior withdrawal of the female 9th tergite/gonocoxite complex, is also consistent with all of the above morphological observations. Under this mechanism, however, the ventral surface of the male 9th sternite is postulated to abut on the proximal ends of the female 9th gonocoxites and the anteroventral angles of the female 9th tergites; subsequent abduction of the male 9th sternite would then lever the entire female 9th tergite/gonocoxite complex posteriorly, rather than simply laterally displace the female 9th gonocoxites.

(5) Spermatophore transfer between the sexes is confirmed by the frequent presence of spermatophore remnants located deep within the bursa in macerated female specimens. The presence of an eversible male gonosaccus has been confirmed by artificial eversion of this structure in macerated male specimens. Eversion of the male gonosaccus directly into the female bursa is inferred from the adjacent alignment of these structures when the terminalia are linked as described above. This conclusion is further supported by [1] the typically deep observed insertion of the spermatophore within the bursa, [2] the presence in several species (i.e., all *Balmes* species and *P. insolens*) of one (or two) pairs of spiculate lobes located on the proximal surface of the everted gonosaccus (these lobes probably serve to anchor the everted gonosaccus within the bursa), and [3] the presence of a hypandrium internum associated with the apex of the gonosaccus (this sclerite probably serves as an insertion site for gonosaccal retractor muscles).

**Taxonomic Differences.**—Several copulatory features appear to be characteristic of all extant psychopsids. These include: (1) presence of a female copulatory fovea to receive the male mediuncus, (2) a means of "trapping" of the female 8th sternite by the male mediuncus and 9th gonocoxites to effect coupling, (3) probable use of the male 9th sternite to expose the female bursal opening, and (4) presence of an eversible male gonosaccus. However, clade-specific differentiation among several details of this generalized copulatory system have also been observed.

These differences may be divided into two classes. First, a "male mediuncus/female copulatory fovea" class, comprised of variations in the detailed configurations of the female copulatory fovea, including the adjacent portions of the 7th and 8th sternites, together with correlated changes in the morphology of the male mediuncus. Several modifications falling into this class have been discussed above. Second, a "male 9th gonocoxite/female 7th or 8th sternite" class, comprised of variations in the details of contact between the male 9th gonocoxites and female sternites during coupling. Variations within this class are discussed below.

A major dichotomy exists between the

Zygophlebiinae and Psychopsinae with regard to the principle female sternite clasped by the male 9th gonocoxites during coupling. In the Psychopsinae, in which a prominent female 8th sternite is present, the male 9th gonocoxites insert under the posterior margin of this sternite; in the Zygophlebiinae, in which the female 8th sternite is reduced, the male 9th gonocoxites insert under the posterior margin of the female 7th sternite.

The zygophlebiine genera *Cabralis* and *Zygophlebius* appear to be transitional between the Psychopsinae and the zygophlebiine genus *Silveira* for this linkage trait. In the former genera a lobate, median, female 8th sternite is present, but, through the combination of a pair of parasagittally protruded female 7th sternite lobes and a pair of distolateral male 9th gonocoxite lobes, the female 7th sternite and male 9th gonocoxites are able to link laterally around the female 8th sternite. In *Silveira* the female 8th sternite is greatly reduced, being present as a narrow transverse bar which lacks setae or protruding lobes. In this genus the male 9th gonocoxites insert under the female 7th sternite, but over (with the female in ventral view) the female 8th sternite. Trapping of the 8th sternite in this case is accomplished by folding the apex of the mediuncus completely beneath 8th sternite, and, presumably, by pressing the sternite against the ventral (rather than dorsal) face of the male 9th gonocoxites. It is interesting to note that all *Silveira* species exhibit a broad, membranous emargination of the male 9th gonocoxites distomedially. This feature ensures that when the sclerotized male 9th gonocoxites are inserted beneath the female 7th sternite they do not interfere with the insertion of the mediuncus into the copulatory fovea, or the adduction of the mediuncus beneath the female 8th sternite. A similar apical male 9th gonocoxite notch is present in *Cabralis*, which allows the 9th gonocoxites to avoid interference with the large, arcuate, copulatory fovea found in that genus.

The linkage system in *Z. leoninus* has apparently diverged in another direction. This species bears a pair of transverse parasagittal scrobes on the posterior margins of the female 7th sternite. These grooves appear to receive during copulation the prominent pair of extrahemigonarcal processes located on the posterior margin of the male gonarcus. However, in *Z. zebra*, which also possess male extrahemigonarcal processes, female 7th sternite scrobes are lacking.

The posterior clasping mechanism in most

psychopsine species is relatively homogeneous, but it has been modified somewhat in the *gracilis* group of *Psychopsis*. The plesiomorphic mechanism involves insertion of the small superprocesses of the male 9th gonocoxites under the posterior margin of the female 8th sternite during coupling. This pattern is found in *Balmes*, the *coelivaga*, *insolens*, and *illidgei* groups of *Psychopsis*, and possibly also *P. gracilis*. However, among the remaining species of the *gracilis* group with known males, i.e., *elegans*, *mimica*, and *barnardi* (males of *dumigani*, *margarita*, *maculipennis*, and *tillyardi* are unknown), the superprocesses appear to be too long to be effectively inserted under the 8th sternite. In these species the elongate superprocesses appear to lie adjacent to the external face of the 8th sternite during coupling, while the posterior margin of this sternite is caught by other smaller lobes near the apex of the gonocoxal arch. For example, in *barnardi* (Figs. 23, 25) and *mimica*, the catch probably consists of the paired structures designated below as the *subprocesses* [Character 25]. It is also possible that the female subgenitale may play a role in the posterior linkage mechanism in this species group.

**Discussion.**—In view of the varied and apparently species-specific nature of the interlocking copulatory elements of male and female psychopsids, it seems likely that these sclerites function as effective prezygotic barriers to interspecific hybridization. However, whether these structures evolved specifically as reproductive isolating mechanisms, or merely fulfill this role as a functional consequence of their gross morphological differentiation, cannot be critically resolved at present.

Although the individual morphological components of psychopsid terminalia had been described in some detail by previous workers, no reference to the copulatory mechanism described here has been found in any prior literature. At least in hindsight this seems surprizing given the simple elegance of the system. Determination of the generality of this or similar copulatory linkage systems within the order Neuroptera is hampered by our inadequate knowledge of copulatory mechanisms in most other families. However, detailed examination of the terminalic structures of the few outgroups used in this study suggests that what might be called "sternal confinement" coupling systems may be widespread within the Neuroptera. For example, in *Polystoechotes punctatus* the male mediuncus and 9th gonocoxites appear to create an

enclosure suitable for confinement of the female subgenitale. In *Nymphes myrmeleonoides* the greatly enlarged posterodorsal process of the male mediuncus seems to insert into a voluminous membranous pouch located midventrally between the posterior margin of the female 6th sternite and the anterior margins of the 7th hemisternites, while the distally forked male 9th gonocoxites confine the posterior margins of the female 7th hemisternites. The largely unexplored character system of male/female coupling mechanisms may hold promise for the identification of characters phylogenetically informative at interfamilial levels of universality, and thus help to resolve the historically elusive phylogeny of neuropterous families.

## OVIPOSITION

**Overview.**—Oviposition is interpreted broadly here to include the set of egg manipulative events occurring between the emergence of an ovum from the ovipore to its release [deposition] by the female. It is suggested here that normally laid psychopsid eggs are actively "powdered" prior to deposition with finely granulated plant and/or mineral material sequestered within the female posterior abdominal chamber. The hypothesized sequence of ovipositional events by which this occurs are given in temporal order below. The numbered events and/or actions correspond to identically numbered sections given under the succeeding heading, "Evidence," where morphological evidence supporting each event/action is presented.

**Oviposition Sequence.**—(1) Prior to the emergence of mature eggs from the ovipore, the female posterior abdominal chamber is actively filled with finely granulated plant and/or mineral material. (2) Eggs emerging from the ovipore are temporarily held at the proximal end of the female 9th gonocoxites, where they are coated with an adhesive secretion(s) derived from the colleterial and/or colleterial accessory glands. (3) "Adhesive" eggs pass to the distal end of the 9th gonocoxites, are inserted into the posterior abdominal chamber, and are powdered with the granulated material contained therein, which adheres to the colleterial gland secretion(s). (4) "Powdered" eggs are removed from the posterior abdominal chamber by the 9th gonocoxites and deposited.

**Evidence.**—(1) Tjeder (1960:172) was apparently the first author to comment on the general presence of large quantities of finely pulverized plant and/or mineral material contained within the abdominal apices of female psychopsids. Tjeder's general observations on African species were corroborated in New's ([1989a]:843) study of Australian psychopsids, and are further attested to here. Similar pulverized materials have been found inside the posterior abdominal chambers of nearly all female specimens of all species I have examined.

Tjeder accounted for the presence of this material by suggesting that it was passively acquired during the process of oviposition in bark crevices. However, several observations suggest that this hypothesis may be faulty. First, I am unaware of any reports of similar materials being held within the abdominal apices of other female neuropterans, even though many are known or strongly presumed to oviposit in similar sites; second, the inflated abdominal apex of psychopsid females does not seem well adapted to insertion in narrow crevices for the purpose of oviposition; third, the abdominal apex of female psychopsids appears to be capable of firm closure, suggesting that passive entry of extraneous materials during oviposition would be unlikely; fourth, the quantity of material typically observed within the abdominal apex would seem to be an acute irritant, if unintentionally acquired, and would probably be expelled before reaching the volumes normally observed; and, fifth, the morphological complexity of the organ within which the material is stored—i.e., a very large membranous sac enclosed within a distinctive bulbous chamber formed by the fusion of three posterior abdominal tergites—would seem to imply a functional connection between the organ and the material contained within it, suggesting a purposeful rather than accidental acquisition of the material. Each of these observations is consistent with the alternative hypothesis that the pulverized materials are actively acquired by the female for sequestration within the chamber, with the likely use of the material as a powdery coating for the eggs.

The hypothesis of active acquisition of the pulverized materials is further supported by other morphological features of the female abdominal apex. One obvious corollary of this hypothesis is the requirement of a mechanism by which such materials may be "internalized," i.e., the abdomen must possess morphological equipment suitable for filling the posterior abdominal chamber. Several observations implicate the 9th gonocoxites in

this role. First, their general location—midventrally between the opposed ventral margins of the 9th tergite, with their posterior apices positioned at the opening of the chamber—is consistent with such a function. Second, their range of motion—a vertical arc around a pair of hinges which loosely join the anterior (proximal) ends of the gonocoxites to the adjacent ipsilateral margins of the 9th tergite—confers upon their posterior (distal) ends the ability to cross through the plane formed by the ventrally opposed 9th tergite margins, and renders them functionally capable of transporting externally gathered pulverized materials into the internal posterior abdominal chamber. Third, at least two ancillary gonocoxite structures further support this view: (1) the presence of "digging" setae on the ventral surface of the 9th gonocoxite stylus, and (2) the presence of a stiffening longitudinal costa running much of the length of each gonocoxite.

*Digging Setae.* All female psychopsids possess a field of strongly modified setae on the ventral surface of each gonocoxite stylus. Within these fields each seta is short, stout, flattened, and slightly concave. Attribution of a digging function to these setae is supported by their overall conformation, their invariable restriction to the ventral surfaces of the styli, and the consistently anterior alignment of their concave faces. While one function of these setae could be the preparation of cavities for egg deposition, another possible function is their use as rasps to dislodge and pulverize fragments of vegetable and/or mineral material from larger semisolid substrata in preparation for its uptake into the posterior abdominal chamber.

*Longitudinal Costae.* The presence of a prominent costa strengthening the longitudinal axis of each 9th gonocoxite is consistent with the use of these sclerites as load bearing organs. While serving as an attachment site for controlling musculature, these costae would also serve to stiffen the gonocoxites and oppose the bending forces associated with lifting (of material into the posterior abdominal chamber) and digging activities.

One final trait which should be mentioned is the dense pilosity associated with the opposed and incurvate posteroventral faces of the female 9th tergite. As suggested by Tjeder (1960:169), these pilose regions undoubtedly act in concert to seal the entry slit into the posterior abdominal chamber with a dense mat of overlapping setae. However, I suggest that their primary function is to prevent the accidental spillage of materials already contained within the chamber, rather than to prevent the unintentional uptake of such materials from the outside.

(2) The psychopsid ovipore opens midventrally between the female subgenitale and the bursal opening, and immediately adjacent to the anterior ends of the 9th gonocoxites. Consequently, eggs emerging from the ovipore pass directly into the anterior end of a sagittoventral canal, the *gonocoxal canal*, which is framed laterally by the symmetrically parasagittal 9th gonocoxites. When situated at the anterior end of the gonocoxal canal the ova lie adjacent to the orifice(s) of the colleterial and colleterial accessory glands, which open sagittally through the membrane forming the canal's roof. Coating an egg thus positioned with adhesive substances would be a simple matter of discharging glandular secretions into the canal, aided possibly by manipulation of the egg by the gonocoxites to spread the secretions. Because of their implication in the production of similar products in other neuropterous families (e.g., Chrysopidae), and the position of their opening(s) in the roof of gonocoxal canal, the origination of adhesive egg coating substances in the colleterial and/or colleterial accessory glands seems likely.

(3) Ova positioned proximally within the gonocoxal canal are separated from the posterior abdominal chamber by the membrane which forms the roof of the canal. However, this membrane is indented distally, resulting in the production of the apices of the gonocoxites as a pair of short free lobes. To enter the posterior abdominal chamber it seems likely that ova pass along the length of the canal until they reach the point where termination of the canal roof permits their insertion into the posterior abdominal chamber by the apices of the 9th gonocoxites. Active control of egg placement within the chamber by the gonocoxites is plausible given the range and direction of gonocoxal motions discussed above.

The primary function of the embowed, cochleariform, suprastylar setae located at the apices of the gonocoxites is uncertain. Two possibilities are: (1) they may facilitate manipulation and/or powdering of ova previously placed within the posterior abdominal chamber, or (2) they may play a role in aggregating materials destined for insertion into the chamber, i.e., they may act as a "broom" to consolidate materials loosened by the digging setae. The typically enlarged, concave, apices of the suprastylar setae and their location immediately

behind the gonocoxal styli (which bear the digging setae) perhaps support the latter role better than the former.

(4) Removal of powdered eggs from the posterior abdominal chamber by the 9th gonocoxites is principally supported by the range of motion of these structures, which allows them to physically transport objects from within the chamber to outside the body.

**Discussion.**—The fact that the postulated final product of the oviposition sequence described above, i.e., eggs coated with pulverized plant and/or mineral materials, is indeed produced in at least some psychopsids is confirmed by Gepp's (1990:136) passing mention of several unpublished observations of the production of such eggs by three different workers (Gepp, Mansell, and Minter), in several African species of *Cabralis* and *Silveira*.

The only published information of which I am aware which might seriously discount the universality of the laying of powdered eggs is Tillyard's account of oviposition in *Psychopsis elegans*. Tillyard ([1919b]:789, 814-815) records the deposition of apparently unpowdered eggs from a captive female of this species. The eggs laid by this female were mostly cemented to an offered cotton-wool substrate. Tillyard's observations are difficult to reconcile with the current morphological finding in *elegans* of a well-developed posterior abdominal chamber filled, as in other psychopsids, with pulverized materials. Tillyard's observations might be explained in several ways. First, powdering of eggs could be under facultative control of the female, rather than obligatory. This might be supported by Gepp's (1990) comment that eggs laid in captivity by some *Silveira* species "*usually* have a sand covering" (italics mine). Second, the laying of unpowdered eggs could be an abnormal behavior induced by unnatural captive conditions. Or, third, Tillyard's female could have been a young lab-reared or wild-caught individual with an empty posterior abdominal chamber. Such a condition, perhaps due to the lack of exposure to a suitable powder source or an age dependency associated with the onset of chamber filling behavior, would necessarily result in unpowdered eggs. Unfortunately, Tillyard's limited comments do not allow confident discrimination among these alternatives.

However, the deposition of uncoated eggs under abnormal captive conditions by some antlion species which normally cover their eggs with a sand coating has been documented (e.g., *Creoleon plumbeus*; see Gepp, 1990: figs. 41 & 42), and this may be the simplest explanation of Tillyard's results.

The ovipositional habits of psychopsids may be unusual in other respects as well. In particular, all extant psychopsids probably oviposit while in flight. While yet unproven, morphological evidence and at least one behavioral observation can be marshalled in support of this hypothesis.

*Morphological Evidence.* The in-flight oviposition hypothesis presupposes the existence of morphological equipment in female psychopsids which is suitable for the manipulation, temporary retention, and subsequent deposition of eggs following their emergence from the ovipore. As argued above, the shape, position, linkage, and range of motion of the 9th gonocoxites implicate these structures as the primary dynamic components in the ovipositional process of psychopsids. Eggs emerging from the gonopore pass directly into the adjacent proximal end of the gonocoxal canal, which is framed laterally by the 9th gonocoxites. As each egg passes down the canal it is coated by secretions from the colleterial glands and, upon reaching the distal end of the canal, is inserted into the posterior abdominal chamber to be coated with granular materials. Following coating, each egg is removed from the chamber by the tips of the 9th gonocoxites, which subsequently release the eggs to effect deposition. This entire process appears to be completely independent of contact with any external surface; and there is little doubt that it could be easily accomplished by a flying female psychopsid.

However, perhaps the most compelling piece of morphological evidence supporting in-flight oviposition is the existence of the remarkable posterior abdominal chamber, which functions as the specialized internal receptacle for carrying egg coating materials. While the benefits of possessing such a chamber are obvious for animals which deposit granularly coated eggs in flight, comparable benefits are difficult to imagine for ground-standing egg depositors. (Psychopsids are here inferred to deposit their eggs on the ground surface because their granularly coated, non-adhesive, eggs appear particularly maladapted for deposition in the elevated sites utilized by many other neuropterous taxa, and because they lack obvious morphological adaptations for egg deposition in crevices [i.e., elongate ovipositors] or below the ground surface [i.e., long narrow abdomens and/or broad fields of digging setae on the abdominal apex].) Such

ground-standing depositors would, presumably, have relatively ready access to granular ground-surface materials near their oviposition sites, and, thus, would appear to be unlikely candidates for the development a specialized internal chamber within which to sequester such materials.

In addition to holding egg-coating materials, the posterior abdominal chamber may also function as a short-term (seconds/minutes) storage site for eggs prior to deposition. However, it seems unlikely that psychopsids routinely use this chamber for longer-term (hours/days) egg storage. The latter assertion is supported by the observation that eggs have never been reported from the macerated posterior abdominal chambers of preserved specimens, even though the usual presence of granular materials within the chambers of these specimens strongly suggests that the vast majority of them were collected during their periods of active oviposition. This observations suggests that each psychopsid egg is individually coated and deposited before the next egg emerges from the ovipore.

Another interesting, but currently unanswerable, question about the precise method of egg deposition in psychopsids is whether the eggs are passively dropped or are actively thrown and/or directed when released. The slender form and proximal articulation of the 9th gonocoxites would appear to be compatible with either method.

Finally, the ubiquity of in-flight oviposition among extant silky lacewings is suggested by the strong similarity in the form of the distal abdominal structures of the females of all species (excluding sternites 7 and 8, and the copulatory fovea, which function as part of the species-specific copulatory apparatus). Intertaxon similarity is particularly striking in two character complexes which are apparently unique to female psychopsids; these are: [1] the presence of the posterior abdominal chamber and the highly fused tritergal framework (8t+9t+ectoprocts) which encloses it, and [2] the presence of a coordinated pair of slender 9th gonocoxites which articulate in a vertical plane around a pair of articulations located on the ventral margins of the 9th tergite. It is difficult to imagine these complex character traits as anything other than adaptations to a single distinctive ovipositional mechanism which is shared by all psychopsids.

*Behavioral Observations.* Probable in-flight egg-deposition behavior has been observed in the field by L. Minter, H. & U. Aspöck, and H. Hölzel, at Ingwe in the South African state of Transvaal. Minter (pers. comm.) reported that the observed behavior consisted of a distinctive jerky, dipping, flight pattern preformed by *Cabralis gloriosus* while flying low over leaf litter. Minter noted that this flight pattern was reminiscent of the in-flight ovipositional behaviors of some dragonflies and tipulids, except that the psychopsid abdomen was never touched to the ground. Although no eggs were recovered or definitely seen to be dropped, the consensus among the observers was that egg deposition was occurring.

Gepp (1990) briefly mentioned the possible existence of in-flight ovipositional behaviors in a few taxa scattered throughout the families Psychopsidae, Nemopteridae, and Myrmeleontidae. The data presented here go far toward demonstrating the existence of this behavior within the Psychopsidae from the standpoint of morphology. However, more detailed field studies of the aerial behavior of psychopsids are still needed to conclusively demonstrate in-flight oviposition in this family. I would encourage neuropterists and/or behaviorists with the capacity to undertake field work when and where psychopsids are present to further investigate this interesting behavioral possibility.

## PHYLOGENETIC ANALYSIS

### METHODS

**Overview.**—Relative phylogenetic relationships among extant psychopsids were estimated cladistically (Hennig, 1981; Wiley, 1981). Sixty characters (147 total character states) were numerically coded for: [1] 21 (of 26; Table 2) extant psychopsid species, [2] eight outgroup species (Table 1), and [3] one hypothetical ancestor. The resulting data set (Appendix 2) was analyzed with the computer program HENNIG86 (Version 1.5; Farris, 1988) to identify minimum length trees and to infer the cladogram mapping of synapomorphic traits. Characters were treated as ordered binary pairs (0 = plesiomorphic, 1 = apomorphic), except as follows (character #-# states-[o]rdered/[u]nordered): 1-5-u; 6-3-o; 8-3-o; 10-3-o; 14-3-o; 16-3-o; 17-3-o; 18-5-u; 22-5-u; 24-3-o; 36-3-o; 38-4-u; 40-3-o; 41-3-o; 45-3-o; 46-3-o; 50-3-o; 51-3-o; 56-3-o; 57-3-o.

**Hypothetical Ancestor and Outgroups.**—Eight outgroup species (Table 1) were initially included

Table 1. Outgroup taxa used in the initial cladistic analysis of the family Psychopsidae, and for the subsequent assignment of character states to the hypothetical ancestor. Species are grouped by superfamilies (sensu Withycombe, [1925]) and families.

| Order<br>    Superfamily<br>        Family | Species |
|---|---|
| Neuroptera | |
|     Hemerobioidea | |
|         Hemerobiidae | *Nomerobius signatus* |
|         Polystoechotidae | *Polystoechotes punctatus* |
|     Osmyloidea | |
|         Osmylidae | *Kempynus falcatus* |
|         Osmylidae | *Osmylus fulvicephalus* |
|     Myrmeleontoidea | |
|         Nemopteridae | *Halter halterata* |
|         Nymphidae | *Nymphes myrmeleonoides* |
|         Nymphidae | *Osmylops armatus* |
| Raphidioptera | |
|     Raphidiidae | *Agulla adnixa* |

in the cladistic analysis as a means of polarizing psychopsid character states. These outgroups were selected as follows: (1) species within the families Hemerobiidae, Poly-stoechotidae, Nemopteridae, and Nymphidae were selected as representatives of the superfamilies "Hemerobioidea" and "Myrmeleontoidea," within which previous authors had placed the family Psychopsidae, (2) species of the family Osmylidae were selected because of their plesiomorphic ocellar configurations, and (3) *Agulla adnixa* was included as a root outgroup lying outside the order Neuroptera.

Hennig86 analyses using the 21 ingroup and 8 outgroup taxa resulted in a single ingroup topology (Fig. 53), but several divergent outgroup arrangements. Except for confamilial outgroup species, which always clustered together, the Nelson consensus tree of the outgroup topologies was completely unresolved. Because the character states used in the cladistic analysis were not explicitly selected with the aim of resolving interfamilial relationships, the different outgroup resolutions obtained in these analyses were judged too speculative for presentation here.

Because no single outgroup taxon was clearly established as the sister group of the Psychopsidae in these initial analyses, a ground-plan outgroup methodology using a single hypothetical ancestor derived from the eight initial outgroups was adopted for the final analysis. Character states

were assigned to the hypothetical ancestor by applying the following rule: for each character assign to the hypothetical ancestor the character state with the broadest distribution among the initially employed outgroup families, i.e., the state found in the highest proportion of the outgroup families (not species). The only exception to this rule was character 1, the inferred polarity of which is discussed in detail under its character treatment below.

## CHARACTERS

The 60 characters and 147 character states included in the cladistic analysis are treated below. Characters are grouped according to major body region, i.e., head, thorax, male terminalia, and female terminalia. Each character treatment is composed of four elements: (1) the character number and name, (2) a brief description of each character state, (3) a Comments section containing notes and discussion pertinent to the character and its states, and (4) a Change List outlining the mapping of the character on the final cladogram (Fig. 53). Change lists are given in the abbreviated format: node#-node#(state#-state#). For example, under Character 1, the notation "10-14(0-1)" is read: Character 1 changes from state 0 to state 1 between cladogram nodes 10 and 14. If a state change occurs on a terminal lineage, the second node# is replaced with the appropriate species name, e.g., "3-

*coelivaga*(1-2)." Whole-family synapomorphies are indicated by the notation "HypAnc-1(state#-state#)," where "HypAnc" represents the hypothetical ancestor used to root the cladogram. In cases where multiple equally parsimonious optimizations of a character are possible on the final cladogram (characters 1, 6, 19, 21, 24, 28, 36, 45, 54, and 56), separate change lists are given for each optimization, with the optimization plotted on the cladogram listed first.

## HEAD (Characters 1-2)

1. Vertex, ocellar/cranial pulvinae.
(0) 3 well-developed ocellar/cranial pulvinae present, 2 dorsolaterals + 1 ventromedial (Tjeder, 1960:175, fig. 341);
(1) 2 distinct ocellar/cranial pulvinae present [dorsolaterals], ventromedial pulvinus either vestigial [its position marked by a few setae or an area of thinned cuticle, e.g., some *Psychopsis*] or absent [lost] (Tjeder, 1960:192, fig. 405; 198, fig. 433);
(2) 0 ocellar/cranial pulvinae present [all lost].

Comments: "Ocelli" have been cited as "vestigial" or "absent" in recent psychopsids (Tillyard, [1919a]; Kimmins, 1939; Tjeder, 1960); however, these works have used the term "ocelli" loosely. The pulvinate, setose, excrescences of the head capsule to which this name has been formerly applied are here called *ocellar/cranial pulvinae*. I suggest, as justified below, that these pulvinae are enlarged manifestations of the small *ocellar pulvinae* upon which neuropterid ocellar corneae are typically borne, rather than modifications of the "ocelli" (i.e., ocellar corneae) themselves.

In the orders Megaloptera and Raphidioptera, sister groups of the Neuroptera (Kristensen, 1981), three ocellar corneae are commonly present and are arranged in the normal pattern (i.e., in an anteriorly directed, bilaterally symmetrical, triangle situated on the cranial vertex above the antennal toruli). Each cornea is borne on the outer side of a small naked prominence, the *ocellar pulvinus*. Within the Neuroptera, distinct ocellar corneae persist only in some osmylids (Link, 1909), where they are borne on the outer sides of presumably homologous, but setose, pulvinae.

Ocellar corneae are absent in psychopsids, but their supporting pulvinae have apparently persisted in most species in the form of 2 or 3 cranial prominences (the ocellar/cranial pulvinae). The partial homology of these prominences with the ancestral ocellar pulvinae is supported by their (1) number [never more than three: 3, 2, or 0], (2) arrangement [an anteriorly directed triangle if 3, a bilaterally symmetrical pair if 2], (3) position on cranium [above and behind the antennal toruli], and (4) setiferousness [as in osmylid ocellar pulvinae]. The large size of psychopsid pulvinae relative to those of megalopterans, raphidiopterans, and osmylids seems best explained by secondary enlargement of the small ancestral pulvinae, whose precise conformation, position, and extent were no longer constrained by the presence of functional ocelli. Cranial pulvinae also occur in the families Dilaridae (e.g., Minter, 1986: fig. 1) and Berothidae (Tjeder, 1959:283, figs. 254-256). Whether these structures also represent partial homologues of ocellar pulvinae requires further study.

Given the broad distribution of ocelli in the Insecta, including the raphidiopterans and most megalopterans, it is reasonable to assume that the presence of ocelli represents a ground plan feature of the Neuropterida. However, their general absence in the Neuroptera, except for some osmylids, is striking and well documented (New, 1989b:54). Because of uncertainty about interfamilial relationships within the Neuroptera it is not currently possible to confidently infer the ocellar state likely to have existed in the immediate ancestor of the Psychopsidae. For the present analysis the hypothetical ancestor has been conservatively coded as state (0). This implies that the ancestor of the Psychopsidae lacked ocellar corneae but bore cranial pulvinae. Given the presence of corneae in some osmylids, however, the presence of corneae in the immediate ancestor of psychopsids cannot be entirely ruled out. The presence of three well-developed ocellar/cranial pulvinae is considered the most plesiomorphic state found within the Psychopsidae, followed by sequential loss of the single median, then the paired dorsolateral, pulvinae.

Change lists: [1] 1-2(0-1), 3-*coelivaga*(1-2), 10-14(0-1); [2] HypAnc-1(0-1), 3-*coelivaga*(1-2), 10-11(1-0).

2. Margin of torulus, medial antennifer.
(0) absent (e.g., Tjeder, 1959:283, fig. 256 [Berothidae]);
(1) present (Tjeder, 1960:175, fig. 341; 192, fig. 405; 198, fig. 433).

Comments: The presence of a single antennifer on the outer lateral rim of each torulus is appar-

ently plesiomorphic within the Neuroptera. The development of a second antennifer on the medial rim of the torulus is a synapomorphy of the Zygophlebiinae.

Change list: 1-10(0-1).

## THORAX (Characters 3-9)

3. Forewing, transverse bilineate fasciae.
(0) absent;
(1) present (New, [1989a]:864, figs. 59-62; 862, fig. 42).

Comments: Presence of these distinctive forewing fasciae has previously been used to distinguish either the genus *Psychopsis* (s.str.), or an informal species group within this genus (Kimmins, 1939; New, [1989a]). In the present analysis they are interpreted as a synapomorphy of the *gracilis* group of *Psychopsis*.
Change list: 5-6(0-1).

4. Forewing, light brown transverse bars.
(0) absent;
(1) present (Tjeder, 1960:193, fig. 412).

Comments: Presence of this barred forewing pattern is interpreted as a synapomorphy of *Zygophlebius*; although the condition found in zns1 differs somewhat from that found in *zebra* and *leoninus*. In zns1 the barring is often rather irregular proximally, and breaks up distally into a mottled pattern reminiscent of a *Silveira* species. In *zebra* and *leoninus* the bars remain approximately concentric and more or less discrete along the length of the wing, but diminish significantly in intensity toward the wing apex (in the distal half of the wing bars are often lacking). The pattern of barring is generally rather faint in all three species.
Change list: 14-15(0-1).

5. Forewing, number of Sc-R1 crossveins.
(0) 1 [but occasionally with 1 or 2 additional adventitious crossveins];
(1) >4 [but rarely <10] (Fig. 32).

Comments: Proliferation of subcostal crossveins (state 1) is tentatively interpreted here as synapomorphy of the Psychopsidae. It should, however, be noted that elevated numbers of subcostal crossveins are encountered sporadically in several other neuropterous families (e.g., Nymphidae, New, 1981; Hemerobiidae, Oswald [1993]). Although the numerous subcostal crossveins in these taxa appear to be the result of parallel increases within the different families, a higher level of universality of this character within the Neuropterida cannot yet be entirely ruled out. In scoring the present character, subcostal crossvein numbers were counted in psychopsids between the base of the subcostal space and the distal closure of the "vena triplica" (by crossvein or Sc-R1 anastomosis), and, in the outgroup species, to a similar distal region of the subcostal space.
Change list: HypAnc-1(0-1).

6. Forewing, crossveins of costal gradate series.
(0) absent or few [mean < or = 5 crossveins/wing] (e.g., New, [1989a]:858, fig. 6);
(1) numerous [mean > 5 crossveins/wing, usually >> 5] (Fig. 32).

Comments: Some psychopsid species exhibit considerable intraspecific variation in costal crossvein number. However, variation across the division number selected here, 5, appears to be rare. Evolution of a well-developed costal gradate series is interpreted here as a synapomorphy of the Psychopsidae, but one which has been secondarily lost independently in *Balmes* and *Zygophlebius* zns1. A second equally parsimonious optimization of this character would interpret the absence of a costal gradate series in the Psychopsidae as plesiomorphic, followed by independent evolution of costal gradate series in the Zygophlebiinae and *Psychopsis*, and its loss (reversal) in *Zygophlebius* zns1. Costal gradate series also occur sporadically in several other neuropterous families (e.g., Hemerobiidae, Myrmeleontidae, Rapismatidae), where they have certainly arisen independently.
Change lists: [1] HypAnc-1(0-1), 2-18(1-0), 15-zns1(1-0); [2] 1-10(0-1), 2-3(0-1), 15-zns1(1-0).

7. Forewing, shape of humeral plate.
(0) compact (Fig. 40);
(1) elongate [intermediate between states (0) and (2)] (Fig. 39);
(2) digitiform (Fig. 38).

Comments: Some species of *Zygophlebius* and *Psychopsis* are characterized by particularly long, digitiform, humeral plates (state 2). A small, compact, plate is here interpreted as the plesiomorphic state (0). Intermediate states (1) occur in *Silveira*, *Cabralis*, and *Zygophlebius* zns1.
Change list: 1-10(0-1), 3-4(0-1), 3-4(1-2), 15-16(1-2).

8. Forewing, width of costal space in pterostigmal region.
(0) narrow [<2 times combined width of adjacent Sc and R1 spaces];
(1) broad [>2 times combined width of adjacent Sc and R1 spaces] (Fig. 32).

Comments: Pterostigmata are absent in all psychopsids. For the purposes of this character the pterostigmal region is taken to be the costal space anterior to the distal portion of the "vena triplica." In all psychopsids the costal space in this region is especially broad. This trait is interpreted as a synapomorphy of the Psychopsidae.
Change list: HypAnc-1(0-1).

9. Hind wing, distal macula.
(0) absent;
(1) present, large, enclosing anastomosis (Fig. 33, b);
(2) present, large, posterior to anastomosis (Fig. 33, d);
(3) present, large, distal to anastomosis (Fig. 33, c);
(4) present, small, directly on anastomosis (Fig. 33, a).

Comments: The presence or absence of a distal hind wing macula has long been used to group species within the Psychopsidae (McLachlan, 1902; Tillyard, [1919a]; Kimmins, 1939). This character is divided here into one absence and four "presence" states, the latter based on the size and position of the macula relative to the "anastomosis" (the distal termination of the "vena triplica"). These states were analyzed as unordered in the cladistic analysis because of a priori uncertainty about their polarity within the family.
The small macula found in *Zygophlebius* species (state 4) is not homologous with the maculae found in *Psychopsis*, s.l. Among the other three presence states, a macula enclosing the anastomosis (state 1) was found to be a synapomorphy of *Psychopsis* (as here defined). States (2) [macula posterior to the anastomosis] and (3) [macula distal to the anastomosis] are interpreted as independent secondary shifts of the macula away from its plesiomorphic position encompassing the anastomosis. These states are synapomorphic of the *gracilis* [state (2)], and *insolens* [state (3)] groups of *Psychopsis*.
Change list: 2-3(0-1), 4-20(1-3), 5-6(1-2), 14-15(0-4).

## MALE TERMINALIA (Characters 10-39)

### 7th and 8th somites (Characters 10-11)

10. Male 8th somite, spiracles.
(0) opening normally through membranous pleural membrane;
(1) opening through secondarily sclerotized regions of the pleural membrane which are dorsally seamlessly continuous with the ventrolateral margins of the 8th tergite (Fig. 1);
(2) opening in the pleural membrane associated with small, free, sclerotized plates (Fig. 6).

Comments: With few exceptions, the spiracles of the psychopsid male 8th somite open through the ventrally extended lateral surfaces of the 8th tergite. The absence of these tergal extensions in *Psychopsis coelivaga* is interpreted as a secondary reversal to the ancestral state (0); while in *Balmes birmanus*, the small sclerotized plates associated with the spiracles of the 8th somite appear to represent vestigial remnants of earlier tergal extensions which have become secondarily divided from the main body of the tergite.
Change list: HypAnc-1(0-1), 3-*coelivaga*(1-0), 19-*birmanus*(1-2).

11. Male 8th sternite, posteromedian lobe.
(0) absent;
(1) present (Fig. 12, pml).

Comments: This character refers to the distinct but inconspicuous, setiferous bulge located sagittally at the apex of the 8th sternite in *Cabralis* and *Zygophlebius*.
Change list: 10-14(0-1).

### 9th somite (Characters 12-27)

12. Male 9th tergite, free posteroventral process.
(0) absent;
(1) present (Fig. 17, pvp).

Comments: In *Cabralis gloriosus* and cns1, the posteroventral angles of the 9th tergite are produced as short angular processes. These processes are a synapomorphy of *Cabralis*.
Change list: 14-17(0-1).

13. Male 9th tergite, costa bracing point of ectoproct articulation.
(0) absent;
(1) present (Fig. 1, bc).

Comments: In all psychopsids the anterior margins of the ectoprocts are broadly hinged to, and loosely articulate with, the posterolateral margins of the 9th tergite. In *Silveira rufus, occultus,* and *marshalli,* the ventral articulation between the ectoproct and 9th tergite is braced by a costa on the inner surface of the 9th tergite. This costa is a synapomorphy of these three species of *Silveira.*
Change list: 11-12(0-1).

14. Male 9th tergite and sternite, articulation.
(0) poorly developed [i.e., tergal and sternal costae bracing articulation either both absent or only one (either) present], or entirely absent;
(1) well developed [i.e., articulation reinforced by both tergal and sternal brace costae] (Figs. 12, 17).

Comments: In the outgroups examined the 9th tergite and sternite are either unarticulated or only weakly articulated. In all psychopsids the anterolateral angles of the 9th sternite articulate directly on the elongate anteroventral angles of the 9th tergite, and both sclerites possess well-developed internal costae bracing the point of articulation. The derived state is interpreted as a synapomorphy of the Psychopsidae.
Change list: HypAnc-1(0-1).

15. Male 9th sternite, anterolateral apodemes.
(0) absent;
(1) present, lying entirely [or principally] in-line [or dorsal] to a line extended anteriorly from the midline of the proximal portion of the lateral costa of the 9th sternite in lateral view (Fig. 12, ala);
(2) present, lying entirely [or principally] ventral to a line extended anteriorly from the midline of the proximal portion of the lateral costa of the 9th sternite in lateral view (Figs. 21 [ala], 30).

Comments: In psychopsids the lateral costae of the 9th sternite are projected anteriorly beyond their points of articulation with the 9th tergite as a pair of short *anterolateral apodemes.* Similar apodemes were absent in the examined outgroups, even where the 9th tergite and sternite were articulated, and their presence in the Psychopsidae is interpreted as a family synapomorphy. The orientation of the anterolateral apodemes differs be-

tween the two psychopsid subfamilies. In the Zygophlebiinae the anterolateral apodemes are largely anterior linear extensions of the lateral apodemes; in the Psychopsinae, the anterolateral apodemes have been displaced ventrally (a synapomorphy of this subfamily).
Change list: HypAnc-1(0-1), 1-2(1-2).

16. Male 9th sternite, shape (ventral view).
(0) not parallel sided or particularly narrow;
(1) narrow and parallel sided (Fig. 2).

Comments: The shape of the 9th sternite exhibits considerable interspecific variation among psychopsids. In the four species of the genus *Silveira* the 9th sternite is especially narrow. In this genus, the anteroventral angles of the 9th tergite are narrowly elongated and inwardly curved. This has resulted in a narrowing of the proximal end of the 9th sternite, and a change in the course of its lateral apodemes from posteriorly convergent to approximately parallel. This correlated set of modifications is considered a synapomorphy of *Silveira.*
Change list: 10-11(0-1).

17. Male 9th sternite, thickness of lateral costa.
(0) lateral costa absent;
(1) thin to moderately thick (Fig. 41);
(2) extremely thick, massive (Fig. 42).

Comments: In all psychopsids the lateral, or sublateral, margins of the 9th sternite are reinforced by internal costae. Although similar costae were found in the outgroup *Polystoechotes punctatus,* most outgroups examined lacked such costae. The presence of these costae in psychopsids is here tentatively regarded as a synapomorphy of the family. In several species of the *gracilis* group of *Psychopsis* (e.g., *elegans, mimica,* and *barnardi*), these costae are greatly thickened (a synapomorphy of these species).
Change list: HypAnc-1(0-1), 6-7(1-2).

18. Male 9th sternite, mesal spurs of lateral costae.
(0) absent;
(1) present, distinct but not robust, aligned with distal portions of lateral costae (Fig. 30);
(2) present, very robust, not aligned with distal portions of lateral costae (Fig. 21).

Comments: In addition to the prominent lateral costae of the 9th sternite, members of the *illidgei* and *gracilis* species groups of *Psychopsis* possess a

spur arising medially from each lateral costa (a synapomorphy of these groups). The form and position of these spurs exhibit some interspecific variation. In the plesiomorphic condition, found in *P. illidgei* and *gracilis*, the spurs are distinct but relatively weakly developed, run more or less longitudinally, are aligned with the distal portions of the lateral costae, and insert at a distinct bend in the lateral costae. In the derived condition, a synapomorphy of *P. elegans, mimica,* and *barnardi,* the spurs are short but very robust, run more transversely, are not aligned with the distal portions of the lateral costae, and do not insert at a distinct bend in the lateral costae.

Change list: 4-5(0-1), 6-7(1-2).

19. Male 9th sternite, configuration of apex.
(0) apex rounded or transverse, largely membranous, without a sagittal emargination (Fig. 7);
(1) apex with a shallow emargination setting off a pair of rounded parasagittal lobes (Fig. 2);
(2) apex robust, with 2-4 prominently protrudent rounded lobes (Fig. 22);
(3) apex elongate and attenuate, tapering to a long filiform process (Fig. 30);
(4) apex bearing a pair of small, angulate, parasagittal cusps separated by a shallow emargination (Fig. 31).

Comments: The conformation of the apex of the male 9th sternite varies extensively among psychopsids. Because no clear polarization was apparent among the observed states, the five states of this character were treated as unordered in the cladistic analysis. The following unambiguous synapomorphies were inferred for states (1) and (4): state (1) is independently derived from state (0) in *Silveira, Zygophlebius zebra + leoninus,* and bns1, and state (4) is derived from state (0) in *Psychopsis coelivaga.* Three equally parsimonious optimizations of states (2) and (3) are possible due to ambiguities in assigning an ancestral state to node 5. The optimization plotted on the cladogram arbitrarily posits the independent derivation of state (3) [in *illidgei*] and state (2) [in the *gracilis* group] from an ancestral state (0).

Change lists: [1] A + B; [2] A + C; [3] A + D; where A = 3-*coelivaga*(0-4), 10-11(0-1), 15-16(0-1), 19-bns1(0-1); B = 5-*illidgei*(0-3), 5-6(0-2); C = 4-5(0-2), 5-*illidgei*(2-3); D = 4-5(0-3), 5-6(3-2).

20. Male 9th sternite, subapical dorsomedial cavity.
(0) absent;
(1) present (Fig. 22, dmc).

Comments: *Psychopsis elegans, mimica,* and *barnardi* each bear a peculiar heavily-walled pit medially on the dorsodistal surface of the 9th sternite. In each of these species, the size and shape of the pit closely corresponds to the size and shape of the distal portion of the mediuncus. This fact, together with the observation that dorsad movement of the 9th sternite apex (resulting from vertical rotation of the 9th sternite around its proximolateral articulations with the 9th tergite) would bring it in close proximity to the mediuncus, strongly suggests that these cavities act as protective recesses for the mediunci. Among the examined species, these pits are restricted to, and constitute a synapomorphy of, *elegans, mimica,* and *barnardi,* although an incipient pit structure appears to be present in *gracilis,* the sister species of this clade. Tjeder (1960:167) casually noted the presence of this structure in *mimica,* and compared it to the "gonapsis" found in some chrysopids. The cladogram (Fig. 53) shows that this structure is clearly derived within the Psychopsidae and is not a homolog of chrysopid gonapses.

Change list: 6-7(0-1).

21. Male 9th gonocoxites, ventral costae.
(0) present, long and prominent, extended at least 1/2 the distance from the gonarcus/9th-gonocoxite articulation to the sagittal midline of the 9th gonocoxites (Fig. 34, vc);
(1) absent, or, at most, a short thickening bracing the gonarcus/9th gonocoxite articulation (Fig. 10, vc).

Comments: In most psychopsids the ventral, or near ventral, margin of each 9th gonocoxite is strengthened internally by longitudinal costa. These costae are reduced or absent (lost) in the three species of the genus *Balmes* and in *Psychopsis illidgei* and *gracilis.* Two equally parsimonious optimizations of this character are possible for the last two species. In the first (plotted on the cladogram), costae are independently lost in *illidgei* and *gracilis*; in the second, costae are lost between nodes 4 and 5, but regained between nodes 6 and 7. In both optimizations, costae are unambiguously lost in *Balmes.*

Change lists: [1] 2-18(0-1), 5-*illidgei*(0-1), 6-*gracilis*(0-1); [2] 2-18(0-1), 4-5(0-1), 6-7(1-0).

22. Male 9th gonocoxites, dorsolateral sclerotized plates.
(0) absent (Fig. 35);
(1) present, proximal portion not flared laterally [or 9th gonocoxite absent] (Fig. 34, dlp);
(2) present, proximal portion flared laterally (Fig. 14, dlp).

Comments: In the presumed plesiomorphic condition (state 1), the gonosaccal membrane inserts on the dorsal margins of the 9th gonocoxites along narrow sclerotized plates lying dorsad of the longitudinal ventral costae. In *Psychopsis elegans*, *mimica*, and *barnardi* these plates are absent (lost) and the gonosaccal membrane arises directly from the dorsal surfaces of the longitudinal costae (state 0). In *Zygophlebius* the sclerotized plates are enlarged, and flared dorsally and laterally (state 2).
Change list: 6-7(1-0), 14-15(1-2).

23. Male 9th gonocoxites.
(0) free, not fused, distally;
(1) fused distally.

Comments: Both free and distally fused 9th gonocoxites are widely distributed states in the Neuroptera. Among examined psychopsids, the 9th gonocoxites are fused distally in all species except *Psychopsis coelivaga*, where their sclerotized apices touch but are not solidly fused. Distally fused 9th gonocoxites are here tentatively regarded as a synapomorphy of the family, while the reversal to an unfused state is regarded as a autapomorphy of *P. coelivaga*.
Change list: HypAnc-1(0-1), 3-*coelivaga*(1-0).

24. Male 9th gonocoxites, superprocesses.
(0) absent or vestigial [or 9th gonocoxites absent] (Fig. 3 [absent]);
(1) present, a pair of short, stout, distal lobes (Fig. 34, spp);
(2) present, a pair of long, narrow, recurved processes (Fig. 23, spp);
(3) present, a pair of inflatable lobes braced by a stout anteromedial costa (Fig. 35, spp);
(4) present, fused, represented by a transverse tumulus crossing the fused 9th gonocoxites distally (Fig. 10, spp).

Comments: In the subfamily Psychopsinae, each 9th gonocoxite bears a erect dorsodistal process either in the form of a small rounded mound or an elongate lobe. Considerable interspecific diversity occurs in these lobes, but, because of their protrudent form, similar points of origination, and general bearing of setae, they are all treated here as homologous states of a common ancestral structure. I follow New ([1989a]) in calling these structures *superprocesses*. It should be noted that the structures to which Tjeder (1960) applied this term in the zygophlebiine genera *Zygophlebius* (figs. 415-416) and *Cabralis* (figs. 436-437) are only analogs; they are not homologs of psychopsine superprocesses, nor are they even homologous processes among the African genera. Tjeder's "superprocessus" in *Zygophlebius* is a modification of the proximodorsal margin of the 9th gonocoxite [Character 22, state 2], while his "superprocessus" in *Cabralis* is a lobe of the posteroventral margin of the gonocoxite.

Because of the lack of any clear polarity among the observed superprocessus states, the five states of this character recognized here were treated as unordered in the cladistic analysis. Nine equally parsimonious optimizations of this character are possible on the cladogram. These are due to ambiguity in the character states assigned to nodes 2 and 7. Because the states of this character were treated as unordered any of three possible states can be assigned to each of these two nodes without affecting the length of the cladogram. The optimization plotted on the cladogram hypothesizes origination of the superprocesses as a pair of stout distolateral lobes in the Psychopsinae [24(0-1)]. In *Balmes* the superprocesses are partially fused medially, and form a transverse tumulus across the apex of the gonocoxites [24(1-4)]. In *Psychopsis mimica* and *barnardi* the superprocesses are slender and extremely elongated [24(1-2)], while in *P. elegans* they are modified to form a pair of enlarged, partially inflatable, lobes braced by a stout costa [24(1-3)].

Change lists: [1] A + D; [2] A + E; [3] A + F; [4] B + D; [5] B + E; [6] B + F; [7] C + D; [8] C + E; [9] C + F; where A = 1-2(0-1), 2-18(1-4); B = 1-2(0-4), 2-3(4-1); C = 2-3(0-1), 2-18(0-4); D = 7-8(1-2), 7-*elegans*(1-3); E = 6-7(1-2), 7-*elegans*(2-3); and F = 6-7(1-3), 7-8(3-2).

25. Male 9th gonocoxites, subprocesses.
(0) absent [or 9th gonocoxites absent];
(1) present (Fig. 25, sbp).

Comments: I use the term *subprocesses* to designate the pair of small lobes adjacent to, but mesad

of, the bases of the superprocesses in *Psychopsis mimica* and *barnardi*. Among the examined species, subprocesses were restricted to, and constitute a synapomorphy of, these species.

Change list: 7-8(0-1).

26. Male 9th gonocoxites, sagittal spines.
(0) absent [or 9th gonocoxites absent];
(1) present (Fig. 28, ss).

Comments: The distally fused 9th gonocoxites of *Balmes* bns1 and *Psychopsis illidgei* each bear a single spinose sagittal process dorsodistally. The process is emarginate apically in bns1, simple apically in *illidgei*. The processes in these species are clearly independently derived structures.

Change list: 5-*illidgei*(0-1), 19-bns1(0-1).

27. Male 9th gonocoxites, paired, projecting, ventrolateral lobes.
(0) absent [or 9th gonocoxites absent];
(1) present (Fig. 10, vll).

Comments: The fused 9th gonocoxite complexes of *Balmes birmanus* and bns1 bear distally a pair of ventrolateral lobes. These prominent structures are here interpreted as a synapomorphy of these two species.

Change list: 18-19(0-1).

**10th [and 11th?] Somites (Characters 28-39)**

28. Male ectoproct, posteroventral shape (lateral view).
(0) one apically rounded lobe (Fig. 12, ect);
(1) one apically truncate lobe (Fig. 37);
(2) two narrowed lobes (Fig. 21, ect).

Comments: Psychopsid male ectoprocts exhibit considerable interspecific variation, but generally bear a single rounded lobe posteroventrally (state 0). The ectoprocts of most members of the *gracilis* group of *Psychopsis* (e.g., *gracilis*, *elegans*, and *mimica*) are characterized by a squared, truncate, apex (state 1). Two species bear clearly bilobed ectoprocts, *Psychopsis illidgei* and *barnardi* (state 2). Transition to a truncate ectoproct form occurs as a synapomorphy of the *illidgei* + *gracilis* groups of *Psychopsis*. This hypothesis suggests that the bilobed ectoprocts of *illidgei* and *barnardi* may have been independently derived through the excavation of the flat distal surface of a truncate ectoproct, rather than by de novo outgrowth of a second marginal lobe. Because the male of *P. tillyardi* is unknown, two equally parsimonious optimizations of this character occur in the vicinity of *P. barnardi / tillyardi*, i.e., transition to a bilobed condition may be an autapomorphy of *barnardi* or a synapomorphy of *barnardi* + *tillyardi*. The former, more conservative, interpretation has been plotted on the cladogram.

Change lists: [1] 4-5(0-1), 5-*illidgei*(1-2), 9-*barnardi*(1-2); [2] 4-5(0-1), 5-*illidgei*(1-2), 8-9(1-2).

29. Male gonarcus, extrahemigonarcal processes.
(0) absent (Fig. 19);
(1) present (Fig. 14, ehgp).

Comments: In *Zygophlebius leoninus* and *Z. zebra*, each extrahemigonarcus bears a prominent posterior process. These processes are unique among extant psychopsids, and constitute a synapomorphy of these species. Tjeder (1960) used the term *entoprocesses* for these structures. I adopt the more general designation *extrahemigonarcal processes* because the cladogram clearly implies that these processes are not homologous with any of the other numerous processes denominated entoprocesses in other neuropterous families.

Change list: 15-16(0-1).

30. Male mediuncus, outline (dorsal view).
(0) not abruptly narrowed near mid-length [or mediuncus absent] (Figs. 24, 27);
(1) abruptly narrowed near mid-length; length of slender apex < length of broad base (Fig. 5);
(2) abruptly narrowed near mid-length; length of slender apex > length of broad base (Fig. 4).

Comments: Progressive narrowing and lengthening of the apical portion of the mediuncus is apparent in the genus *Silveira* (i.e., *jordani*, *rufus*, *occultus*, *marshalli* [least to most apomorphic]). State (1) is a synapomorphy of the species *rufus*, *occultus*, and *marshalli*, in which the apical portion of the mediuncus has become abruptly narrowed with respect to its broad base. State (2), in which the narrowed apical portion of the mediuncus has become elongated, and—at least in *marshalli*—further narrowed, is a synapomorphy of *occultus* and *marshalli*.

Change list: 11-12(0-1), 12-13(1-2).

31. Male mediuncus, proximodorsal lobes.
(0) one pair of small dorsolateral lobes present near mid-length (Fig. 3, dll);
(1) lobes absent [or mediuncus absent] (Fig. 8);
(2) one pair of large parasagittal lobes present proximally (Fig. 26, psl).

Comments: One pair of symmetrically protruding lobes is present on the dorsal surface of the mediuncus in *Psychopsis illidgei* and *Silveira rufus, occultus,* and *marshalli.* Based on differences in the formation and insertion of these lobes, these lobes are here interpreted as independent developments in *Silveira* (state 0) and *Psychopsis* (state 2).
Change list: 5-*illidgei*(1-2), 11-12(1-0).

32. Male mediuncus, apex (dorsal view).
(0) simple [or mediuncus absent] (Figs. 4, 15);
(1) bifid or emarginate (Figs. 9, 27).

Comments: As noted by New ([1989a]:843), mediuncal apices of extant psychopsids are either simple [African species] or bifid [Australian and Asian species]. Both states occur widely in other neuropterous families. Based solely on the outgroups used for this study, a simple apex is tentatively assumed to be the plesiomorphic state within the Psychopsidae. Under this interpretation, a bifid apex constitutes a synapomorphy of the Psychopsinae.
Change list: 1-2(0-1).

33. Male mediuncus, apex (lateral view).
(0) linear, recurved, or weakly decurved relative to base [or mediuncus absent];
(1) strongly decurved relative to base, forming a long, stout, hook (Fig. 19, med).

Comments: The distal portions of the mediunci of *Cabralis gloriosus* and cns1 are compressed and strongly decurved, forming a flattened hook. This state is a synapomorphy of *Cabralis.*
Change list: 14-17(0-1).

34. Male mediuncus, distal end (lateral view).
(0) not recurved [or mediuncus absent];
(1) distinctly recurved (Fig. 14, med).

Comments: The presence of a subapically recurved mediuncus is a synapomorphy of the genus *Zygophlebius.* Progressively enhanced recurvature of the distal portion of the mediuncus is apparent within this genus (i.e., zns1, *zebra, leoninus* [least to

most recurved]).
Change list: 14-15(0-1).

35. Male mediuncus, dorsodistal surface (transverse section).
(0) convex [or mediuncus absent or bifid];
(1) concave (Fig. 16).

Comments: In *Zygophlebius zebra* and *leoninus* the dorsal surface of the recurved mediuncal apex is distinctly impressed (i.e., concave in transverse section). This feature is a synapomorphy of these two species.
Change list: 15-16(0-1).

36. Male mediuncus, apodeme of mediuncal adductor muscle.
(0) absent [or mediuncus absent];
(1) present, inserting proximoventrally on floor of mediuncus (Figs. 19 and 23, ama);
(2) present, inserting at base of terminal mediuncal cleft (Fig. 26, ama).

Comments: In psychopsids, a mediuncal adductor muscle is postulated to insert on an apodeme arising from either the proximoventral floor of the mediuncus (African species and *Psychopsis barnardi*), or the base of the apical mediuncal cleft (Australian and Asian species, except *P. barnardi*). None of the outgroups examined possessed a distinct mediuncal adductor apodeme. The development of an adductor apodeme attached to the floor of the mediuncus (state 1) is interpreted a synapomorphy of the Psychopsidae; and the migration of this apodeme to the base of the terminal cleft (state 2) is interpreted as a synapomorphy of the subfamily Psychopsinae.

The condition found in *P. barnardi* is apomorphic (a reversal) with respect to other *Psychopsis* species. In this species a large rounded lobe has developed between the apodeme and its plesiomorphic insertion at the base of mediuncal cleft; this has resulted in secondary displacement of the adductor apodeme to the floor of the mediuncus. Because the male of *tillyardi* (sister species of *barnardi*) is unknown, the cladogram position of this reversal is ambiguous. It may represent an autapomorphy of *barnardi,* or a synapomorphy of *tillyardi + barnardi.* Although the deep median depression of the posterior margin of the female 7th sternite in both species strongly suggests that the male of *tillyardi,* when discovered, will possess a mediuncal configuration similar to that of *barnardi,* I have conser-

vatively plotted this reversal on the cladogram as an autapomorphy of *barnardi*.

Change lists: [1] HypAnc-1(0-1), 1-2(1-2), 9-*barnardi*(2-1); [2] HypAnc-1(0-1), 1-2(1-2), 8-9(2-1).

**37. Male mediuncal accessory sclerites.**
(0) absent [or mediuncus absent];
(1) present (Figs. 14 and 26, mas).

Comments: The genitalic armature of all psychopsid males includes a pair of elongate mediuncal accessory sclerites. These sclerites are oriented longitudinally in the gonosaccal membrane, and are positioned bilaterally at the base of the mediuncus. The sclerites are generally weakly sclerotized and diffusely margined. Proximally, they are closely associated, or continuous, with the proximal end of the mediuncus; distally, they are either free or loosely fused below the extragonopons. These sclerites may provide additional sites for the insertion of muscles controlling the movement of the mediuncus. Their presence is interpreted a synapomorphy of the Psychopsidae.

Change list: HypAnc-1(0-1).

**38. Male hypandrium internum, angle between dorsal margin and distal portion of "keel" (lateral view).**
(0) << 90 degrees (Tjeder, 1960:195, fig. 418);
(1) approximately 90 degrees (Fig. 36);

Comments: The derived state is a synapomorphy of the *insolens*, *illidgei*, and *gracilis* groups of *Psychopsis*. No hypandrium internum was present in the nemopterid outgroup *Halter*.

Change list: 3-4(0-1).

**39. Male gonosaccal membrane, rounded spiculate lobes.**
(0) absent;
(1) present (Fig. 11).

Comments: The three species of the genus *Balmes*, and *Psychopsis insolens*, each bear a pair of small, but distinct, spiculate lobes ventrolaterally on the everted gonosaccus near its base. At rest, the lobes are withdrawn within the inverted gonosaccus. It seems likely that these lobes function as friction pads to grip the female and stabilize the base of the gonosaccus while it is everted during copulation and insemination. The lobes in *Balmes* and *Psychopsis* are interpreted here as paral-

lel developments. In *Balmes terissinus*, a second smaller pair of lobes is present on the dorsal surface of the gonosaccus.

Change list: 2-18(0-1), 20-*insolens*(0-1).

## FEMALE TERMINALIA (Characters 40-60)

### 7th and 8th somites (Characters 40-46)

**40. Female 7th sternite, posterior margin.**
(0) transverse and simple, without a sagittal emargination, process, or depression;
(1) with a medial emargination and/or depression (Figs. 49, 51);
(2) with a medial emargination and a sagittal process, the latter [sometimes small] representing the posterior termination of a short midventral carina (Fig. 44, mvc).

Comments: Derived state (1) is characteristic of all female psychopsids and is considered a family synapomorphy. Derived state (2) is a further synapomorphy of *Zygophlebius*.

Change list: HypAnc-1(0-1), 14-15(1-2).

**41. Female 7th sternite, posterior margin.**
(0) without a small sagittal cusp at the bottom of a deep depression;
(1) with a small sagittal cusp at the bottom of a deep depression (Fig. 49).

Comments: State (1) is a synapomorphy of *Psychopsis barnardi* + *tillyardi* (see also Comments under Character 45).

Change list: 8-9(0-1).

**42. Copulatory fovea between female 7th and 8th sternites.**
(0) absent;
(1) present (Figs. 44, 49, 51).

Comments: All female psychopsids possess a copulatory fovea located between (and sometimes extended onto) the 7th and 8th sternites. This depression/pit receives the distal portion of the male mediuncus during copulation and is a distinctive synapomorphy of the family Psychopsidae.

Change list: HypAnc-1(0-1).

**43. Female 7th and 8th sternites.**
(0) not fused [or 8th sternite absent (lost, not fused)] (Figs. 49, 51);
(1) fused.

Comments: State (1) is independently derived in *Balmes* and *Psychopsis illidgei*. In other psychopsids the adjacent margins of the female 7th and 8th sternites are membranously articulated, although often closely adpressed.

Change list: 2-18(0-1), 5-*illidgei*(0-1).

44. Female 8th sternite.

(0) present, hemiannular, unmodified;

(1) present, a small compact median sclerite with 1 or 2 distal lobes (Fig. 44);

(2) present, a narrow, transversely elongated sclerite (Tjeder, 1960:190, fig. 399);

(3) present, a bilaterally symmetrical, broadly triangular or trapezoidal sclerite with lateral margins marked by thickened internal costae (Figs. 49, 51).

Comments: The 8th sternites of the examined outgroups may be characterized as follows: [1] *Agulla*, homology uncertain, absent [presumed lost], or possibly homologous with a transverse, invaginated and sclerotized strip associated with the posterior margin of sternite 7, [2] *Nomerobius*, *Nymphes* and *Polystoechotes*, absent [presumed lost], [3] *Halter*, present, hemiannular, unmodified, [4] *Osmylops*, present, a pair of sagittally divided hemisternites, and [5] *Osmylus* and *Kempynus*, present, a transverse bar bearing posterolateral lobes. A distinct 8th sternite is present in all female psychopsids (Tjeder, 1960:174 incorrectly states that it is absent in *Silveira*, where it is present but reduced), but the outgroup states bear little resemblance to any psychopsid state. For the purpose of the cladistic analysis, the hypothetical ancestor has been assigned an unmodified, hemiannular, 8th sternite condition. This state is probably plesiomorphic within the Neuroptera. Among the outgroups, this state most closely resembles the condition found in the nemopterid *Halter*. The states of this character were treated as unordered in the cladistic analysis.

Under the assumptions above, modification of the 8th sternite to a narrowed, transverse, sclerite (state 2) is a psychopsid family synapomorphy, even though similar modifications have occurred in other families. Further modification of the 8th sternite into a compact median prominence (state 1) is a synapomorphy of *Cabralis* + *Zygophlebius*. Secondary enlargement of sternite 8 to form a triangular or trapezoidal structure is a synapomorphy of the *illidgei* + *gracilis* groups of *Psychopsis*.

Change list: HypAnc-1(0-2), 4-5(2-3), 10-14(2-1).

45. Female 8th sternite, small medial cusp of anterior margin.

(0) absent [or 8th sternite absent];

(1) present, apex directed dorsally [inwardly], anteromedian face of sternite without a deep rounded concavity (Figs. 51, 52);

(2) present, apex directed ventrally (outwardly) or anteriorly, anteromedian face of sternite with a deep rounded concavity (Figs. 49, 50).

Comments: In the *illidgei* and *gracilis* groups of *Psychopsis* the female copulatory fovea is comprised of a pit formed primarily from the adjacent depressed margins of the medial portions of the 7th and 8th sternites, rather than a membranous or secondarily sclerotized pit between these sclerites. Within the *gracilis* group there is an evident transformation in the location of the main depression of the fovea, from an intersternal, or 7th sternal, position to its location principally on the anteromedial face of sternite 8. This process appears to begin with the anteromedian attenuation of the 8th sternite, and, sagittally, its inward deflection as a narrow cusp (state 1), followed by the development of a secondary depression posterior to the cusp, which effectively alters the orientation of the cusp itself (state 2).

State (2) is a synapomorphy of *Psychopsis tillyardi* + *barnardi* in which the anteromedian 8th sternite cusp overlaps the posteromedian cusp of the 7th sternite. The secondary depression behind the 8th sternal cusp in females of *barnardi* correlates with, and is certainly an adaptation or coadaptation to, the presence of a large distoventral lobe of the mediuncus in males of this species (Figs. 49, 50). The presence of a similar depression in *tillyardi* strongly suggests that a similar mediuncal lobe will be found in the presently unknown male of *tillyardi*. Because no females of *gracilis* were available for examination, the universality of state (1) is uncertain. It may be a synapomorphy of the entire *gracilis* group, or of the *gracilis* group except *gracilis*. Lacking knowledge of the state in *gracilis*, the latter, more conservative, interpretation has been plotted on the cladogram.

Change lists: [1] 6-7(0-1), 8-9(1-2); [2] 5-6(0-1), 8-9(1-2).

46. Female 8th and 9th tergites.
(0) not fused;
(1) fused (Fig. 43).

Comments: In all female psychopsids tergites 8 and 9 are solidly fused along their adjacent lateral margins; this condition is synapomorphy of the family.
Change list: HypAnc-1(0-1).

### 9th and 10th [and 11th?] Somites (Characters 47-60)

47. Female 9th tergite, anterolateral apodemes.
(0) absent;
(1) present (Fig. 43, ala).

Comments: All female psychopsids possess a bilaterally symmetrical pair of short, broad, apodemes issuing from the 9th tergite antecosta dorsad of the 8th somite spiracles; this condition is synapomorphy of the Psychopsidae. Muscles attached to these apodemes are almost certainly responsible for adduction of the fused 8th tergite/9th tergite/ectoproct complex which terminates the female abdomen.
Change list: HypAnc-1(0-1).

48. Female 9th tergite, pilose posteroventral border.
(0) absent;
(1) present (Tjeder, 1960:203, fig. 441).

Comments: The posteroventral margins of tergite 9 in all female psychopsids are inwardly revolute, sagittally adpressed, and densely pilose. This condition is a family-level synapomorphy.
Change list: HypAnc-1(0-1).

49. Female 9th tergite, distal apodemes.
(0) absent;
(1) present (Fig. 43, da).

Comments: All female psychopsids possess a bilaterally symmetrical pair of slender apodemes issuing from near the dorsal angles of the posteroventral 9th tergal lobes; this condition is a synapomorphy of the Psychopsidae. Muscles presumed to attach to these apodemes probably help to control the position of the inwardly revolute posteroventral margins of the 9th tergite. These apodemes are sometimes difficult to locate, even in stained preparations.

Change list: HypAnc-1(0-1).

50. Female 9th gonocoxite, overall shape.
(0) more or less reniform;
(1) spathulate (Fig. 43, 9gcx).

Comments: The derived state is a distinctive synapomorphy of the family Psychopsidae.
Change list: HypAnc-1(0-1).

51. Female 9th gonocoxite, longitudinal costa.
(0) absent;
(1) present (Tjeder, 1960:179, fig. 361, ap).

Comments: This costa, found in all female psychopsids, stiffens the longitudinal axis of the 9th gonocoxite. The derived state is tentatively interpreted here as a family synapomorphy. Although the possibility of a higher level of universality for the derived state cannot be entirely dismissed (note its presence in some, but not all, outgroup taxa), its simple functional structure, scattered distribution among neuropterous family-level taxa, and the widely differing conformations of female 9th gonocoxites in these families suggest that longitudinal costae may have evolved independently in several different neuropterous families.
Change list: HypAnc-1(0-1).

52. Female 9th gonocoxite, longitudinal row of stiff setae.
(0) absent;
(1) present (Tjeder, 1960:179, fig. 361).

Comments: The 9th gonocoxites of *Silveira* species each bear a prominent longitudinal row of stiff setae lying ventral to, and following the course of, the longitudinal costa of the 9th gonocoxite. This row of setae is absent in other psychopsids.
Change list: 10-11(0-1).

53. Female 9th gonocoxite, aggregation of setae near insertion of stylus.
(0) absent;
(1) present (New, [1989a]:883, fig. 220, cs; 871, fig. 131).

Comments: The derived state is a synapomorphy of *Psychopsis*. Species of this genus bear a fairly tightly clustered aggregation of stiff setae adjacent to the insertion of the 9th gonocoxite stylus. This setal group is distinct from both the dense group of "suprastylar" setae [Character 54] at the apex of the 9th gonocoxites, and the more scattered proximal

and ventral setae of this sclerite.

Change list: 2-3(0-1).

54. Female 9th gonocoxite, suprastylar setae.
(0) all apically unmodified acuminate setae;
(1) >50% apically unmodified acuminate setae, with at least a few elongate cochleariform setae ventrally (Tjeder, 1960:179, fig. 361);
(2) >50% cochleariform setae, generally with at least a few apically unmodified acuminate setae dorsally.

Comments: All female psychopsids bear a dense group of arched setae clustered at the distal (posterior) apex of the 9th gonocoxites. I refer to these as "suprastylar" setae (= "dorsal setae" + "ventral setae" of New, [1989a]:883, fig. 220), from their position above the gonocoxal stylus. These setae are of two forms: arched acuminate and arched cochleariform (i.e., spoon-shaped; see Tjeder, 1960:196, fig. 425). When both setal forms are present (most species) the transition between them is gradual, with the more ventral setae (i.e., closer to the gonocoxal stylus) more highly cochleariform.

Two equally parsimonious optimizations of this character are possible on the cladogram. Both optimizations interpret the evolution of cochleariform suprastylar seta (state 1) as a psychopsid synapomorphy; but, one optimization interprets the occurrence of state (2) in *Cabralis* + *Zygophlebius* and the Psychopsinae as two independent proliferations of cochleariform setae, while the second optimization accounts for the observed character distribution by postulating state (2) also as a family-level synapomorphy, followed by reduction in the numbers of cochleariform setae in *Silveira*. The former interpretation has been arbitrarily plotted on the cladogram.

Change lists: [1] HypAnc-1(0-1), 1-2(1-2), 10-14(1-2); [2] HypAnc-1(0-1), HypAnc-1(1-2), 10-11(2-1).

55. Female 9th gonocoxite stylus, short stout setae.
(0) absent [i.e., stylus setae acuminate, or stylus absent];
(1) present (Tjeder, 1960:179, fig. 361; 196, fig. 424).

Comments: All female psychopsids possess a field of stout, dished, "digging" setae, which are restricted to the ventral surfaces of the gonocoxal styli. This trait is here interpreted as a family synapomorphy. Somewhat similar terminalic setae have been reported in a few other neuropterous families (e.g., Stange, 1970:37, fig. 14, and Miller, 1990 [Myrmeleontidae]; Adams, 1967:235, figs. 20-

21 [Chrysopidae]); however, they are not to my knowledge known from the gonocoxal styli of any other family. Although a specific function has not been demonstrated for these setae, their stout construction, concave and parallelly oriented anterior faces, distal location on the 9th gonocoxites, and insertions restricted to the venter of the gonocoxal styli, are all consistent with a function analogous to the teeth on a rasp, and are most likely used to loosen fine particulate matter for subsequent transfer to the posterior abdominal chamber [Character 60].

Change list: HypAnc-1(0-1).

56. Female bursa, number of inserted bursal accessory gland ducts.
(0) 1 unpaired duct;
(1) 1 pair of ducts (Tjeder, 1960:203, fig. 448, ag);
(2) 2 pairs of ducts (Tjeder, 1960:196, figs. 429 and 430, ag).

Comments: Bursal accessory glands have been reported in most families of Neuroptera, and were first elaborated upon in the Psychopsidae by Tjeder (1960), as "glandulae accessoriae." These exocrine glands insert on the distal end of the bursa by means of narrowed ducts, and are distinct from the proximomedian colleterial and colleterial accessory glands, which are also present in psychopsids. The apparent relative dorsal/ventral and lateral points of insertion of the bursal accessory gland ducts often vary with the degree of inflation of the bursa (e.g., whether spermatophore remnants are present or absent). These glands were found to be present in all examined psychopsids. They were incorrectly cited as absent in *Silveira* and *Psychopsis* by Tjeder (1960:174, 206) and in *Psychopsis* (including *Balmes*) by New ([1989a]:844]). In macerated specimens, careful preparation and staining are often necessary to detect these glands. A single pair of glands is probably plesiomorphic within the Neuroptera, and this state was found in all examined psychopsids, with the following two exceptions: (1) two pairs of glands and ducts are present in, and synapomorphic of, the clade *Zygophlebius zebra* + *leoninus*, and (2) in *Balmes birmanus* the bursal accessory gland ducts are partially fused, and reach the bursa as a single, common, median duct. The latter state is plotted on the cladogram as an autapomorphy of *B. birmanus*, but it may be a synapomorphy of the clade *birmanus* + bns1 (the female of the latter species is unknown). A charac-

ter state apparently intermediate between the partially fused bursal ducts of *birmanus* and the more widely separated duct insertions of non-*Balmes* psychopsids occurs in *Balmes terissinus* (sister-species of the *birmanus* + bns1 clade), where two distinct, but very closely adjacent, duct insertions are present.

Change lists: [1] 15-16(1-2), 19-*birmanus*(1-0); [2] 15-16(1-2), 18-19(1-0).

## 57. Female bursa, lateral corniform diverticulae.
(0) absent;
(1) present (Fig. 47; Tjeder, 1960:196, fig. 430).

Comments: In most psychopsids the narrow ducts of the bursal accessory glands insert without enlargement onto the more or less planar surface of the bursa. In *Zygophlebius* each of the plesiomorphic pair of ducts inserts on a distinctly enlarged, attenuate, smooth-walled, distolateral lobe of the bursa. These structures, here called *corniform diverticulae* in reference to their shape, are clearly present in all three *Zygophlebius* species, but are particularly well developed in *leoninus*. Tjeder (1960:197) called these structures the "accessory structures . . . of the spermatheca." Corniform diverticulae are here considered a synapomorphy of *Zygophlebius*, but they may be incipient in *Cabralis*. In *Z. zebra* and *leoninus*, the ducts of the second pair of bursal accessory glands insert on the lateral walls of the corniform diverticulae.

Change list: 14-15(0-1).

## 58. Female spermatheca, ventrolateral lobes.
(0) absent;
(1) present, broad in lateral view (Fig. 46, vll);
(2) present, narrow in lateral view (Tjeder, 1960:179, figs. 363, 365).

Comments: All zygophlebiine species possess a pair of hollow ventrolateral lobes near the proximal end of the spermatheca. The presence of these lobes is here interpreted as a synapomorphy of this subfamily. It is further suggested that the narrow lobes of *Silveira* represent a secondarily constricted, and thus synapomorphic, form of the plesiomorphically broad lobes found in *Cabralis* and *Zygophlebius*. However, it should be noted that the absence of these spermathecal lobes in the Psychopsinae, and their observed distribution within the Zygophlebiinae, renders identification of the plesiomorphic zygophlebiine state somewhat arbitrary.

Change list: 1-10(0-1), 10-11(1-2).

## 59. Female spermatheca, lamellate apodemes extending from lateroventral margins.
(0) absent;
(1) present (Fig. 48, lap).

Comments: The derived state is interpreted as a synapomorphy of the *illidgei* and *gracilis* groups of *Psychopsis*. These plates probably function as surfaces for the insertion of muscles which consolidate the position of the spermatheca within the female abdomen. Enlarged lamellate plates extending from the sides of the spermatheca are absent in other psychopsids.

Change list: 4-5(0-1).

## 60. Female posterior abdominal chamber.
(0) absent;
(1) present (Fig. 43, pacm [artificially everted]).

Comments: The presence of a large membranous sac lining the hollow formed by the fused female 8th and 9th tergites and ectoprocts is a conspicuous synapomorphy of the family Psychopsidae. This sac encloses a large internal space, here called the *posterior abdominal chamber*, at the posterior end of the female abdomen. Tjeder (1960:168-169, 172) discussed this space under the name "genital chamber," and stated that it was confluent with the "spermatheca" (bursa + spermatheca as used here) by a wide membranous duct—the purported duct being shown in each of Tjeder's figures of the bursa-spermatheca complex of African psychopsids (i.e., Tjeder, 1960: figs. 363, 371, 387, 402, 427, 447) as a ductiform attenuation of the membranous bursa diverging from the proximal end of the sclerotized spermatheca. No such duct exists. In all psychopsids I have examined, the bursa simply opens through the ventral wall of the abdomen posterior to the subgenitale and between the bases of the ninth gonocoxites; it has no direct internal connection to the posterior abdominal chamber. Since the bursa and the chamber lack a connecting duct, it seems more appropriate to designate the chamber by the more generic phrase "posterior abdominal chamber," than the term "genital chamber."

Change list: HypAnc-1(0-1).

## OMITTED CHARACTERS

Several characters used in earlier taxonomic works have been intentionally omitted from the suite of traits employed here to infer phylogenetic relationships within the Psychopsidae. A few of the more prominent of these characters are discussed below to document the reasons for their omission.

**Vena Triplica** (Fig. 32).—Tillyard ([1919a]) and subsequent authors have emphasized the presence of a venational configuration termed the "vena triplica" as a diagnostic feature of psychopsid neuropterans. According to Tillyard ([1919a]:754), this fore- and hind wing feature is formed by the "parallel" and "strengthened" basal two-thirds to three-quarters lengths of the three longitudinal veins "Sc, R [=anterior radial trace, =R1 of authors], and Rs [=anterior sectoral trace]," which are joined distally (at the "anastomosis") by crossveins or brief fusions of the longitudinal veins themselves.

After considerable reflection upon the nature of the vena triplica, I have at length concluded that it cannot be considered a psychopsid synapomorphy. Although this feature constitutes an important part of the psychopsid wing gestalt, the derived aspects of the psychopsid wing which might be associated with the vena triplica in fact seem to be due more to contrasts between the vena triplica and its surrounding venation than to the vena triplica itself. Specifically, two conditions—(1) the consistently broad forewing and hind wing costal spaces, and (2) the apparently abrupt termination, at the anastomosis, of the linearity of the longitudinal veins which comprise the vena triplica [due to localized vein fusion or constrictive crossvenation occurring at this point]—strongly enhance the visual perception of the vena triplica as a distinct entity, by acting to isolate it from the margins of the wing.

In other neuropterous families in which the proximal portions of the subcosta, anterior radial trace, and anterior sectoral trace are similarly parallel and robust (e.g., many osmylids, polystoechotids, ithonids, rapismatids, and dilarids), the visual impression of these veins is considerably different. This difference appears to be due to a visual perception of their continuation or association with the margin of the wing. This may be effected in a number of different ways, for example: (1) a consistently narrow costal space hinders visual differentiation of the three veins as an entity distinct from the anterior margin of the wing, (2) a basally wide but distally narrowed costal space presents a visual perception of the veins becoming confluent with the wing margin near the anterior aspect of its apex, and (3) a clear fusion of two or more of the veins distally often (e.g., many myrmeleontoid taxa) leads to the visual perception of a common fused vein continuing to near the wing apex. In each of these cases, unlike the condition found in psychopsids, potential isolation of the three veins is diminished by a visual tie to the wing margin.

Thus, psychopsid wings appear to differ from those of other neuropterans not in the possession of a vena triplica per se, but rather, in the possession of a consistently broad costal space and of branching patterns of the subcosta, anterior radial trace, and anterior sectoral trace which are distinctly different proximal and distal to the anastomosis.

**Allometric Forewing Elements.**—Froggatt (1903) and subsequent authors (e.g., Tillyard, [1919a]; Kimmins, 1939; New, [1989a]) have all noted the presence of a "raised" or "embossed" area at the apex of the forewing vena triplica in *Psychopsis illidgei*. These authors have employed this character consistently as a diagnostic feature of the genus *Megapsychops*. Rather than a "true" embossment (as found, for example, on the forewings of *Loyola croesus* [Chrysopidae] and *Gayomyia falcata* [Hemerobiidae]), this "raised" area appears to be simply part of an arcuate folding of the wing surface caused by localized allometry in forewing growth within the genus *Psychopsis*. This interpretation is consistent with the following observations. First, the four specimens of *illidgei* I have examined show a positive correlation between fold prominence and increasing forewing length. Second, similar but less developed folds occur at topographically homologous positions in the forewings of other moderate-sized *Psychopsis* species, e.g., *elegans*, *mimica*, *barnardi*, and *tillyardi*; and fold prominence in these species is typically more pronounced in larger individuals. Third, as the largest psychopsid species in terms of wing dimensions, *illidgei* would be expected (as observed) to exhibit fold development exceeding that of other species within the genus. Fourth, the smaller species of *Psychopsis*, e.g., *coelivaga*, *meyricki* and *insolens*, generally lack evidence of fold development.

The absence of evidence of fold development in African and Asian psychopsids, even within the genus *Silveira* where considerable interspecific variation in forewing size is apparent, suggests

that the allometry has been derived only within *Psychopsis*.

A second forewing feature which appears to exhibit allometric variation within *Psychopsis* is the state of the tornus, which generally becomes more pronounced, i.e., angular, with increasing wing size (Tillyard, [1919a]). Both tornal and fold characters have been omitted from the phylogenetic analysis because their apparent allometry suggests that variation observed in these traits is not phylogenetically significant at interspecific levels of universality.

**Forewing Venation.**—Kimmins (1939) made extensive use of the arrangement of forewing veins M and Cu to diagnosing psychopsid genera. Character states employed by Kimmins included the presence or absence of fusion between these veins, and, in the former cases, the length of fusion. More recent workers (Tjeder, 1960; New, [1989a]) have de-emphasized this trait. Examinations of this character undertaken for the present work revealed considerable intraspecific variation in Kimmins' states of this character. Consequently, it has been omitted from the phylogenetic analysis. High levels of intraspecific variation in the "completeness" of the various fore- and hind wing gradate series has also lead to their deletion from the analysis.

## RESULTS

The cladistic analysis of coded character data (Appendix 2) for the 21 psychopsid (ingroup) species and the hypothetical ancestor resulted in the single minimum length tree shown in Fig. 53 (length = 104 steps). This cladogram represents the first detailed hypothesis of intergeneric and intrageneric relationships within the family Psychopsidae. Cladogenetic relationships within the family are well resolved on this cladogram. Both its consistency index (.83) and retention index (.91) are relatively high; and the majority of superspecific clades are supported by two or more synapomorphies. The monophyly of the entire family is particularly well supported with 22 synapomorphies.

## CLASSIFICATION

Given its small number of extant species, the intrafamilial classification of the Psychopsidae has been surprisingly controversial over the last 75 years, particularly at the generic level. In the sections below I propose a new family- and genus-

group classification for the Psychopsidae and discuss its merits relative to earlier classifications.

**New Classification.**—The classification of extant psychopsids shown in Table 2 is newly proposed here. Except where otherwise noted, it is used herein as the basis of taxonomic discussions. The classification is fully "sequenced" (Wiley, 1981) for the 21 examined species. Sequencing allows a set of hypothesized branching relationships (in this case the cladogenetic relationships shown in Fig. 53) to be encoded in the form of a classification, with the encoded relationships being fully recoverable from the classification by the application of a few simple rules (see Wiley, 1981). Asterisked (*) species have not been seen. Consequently, their positions in the phylogenetic sequence are unsubstantiated. These species have been arbitrarily placed in the phylogenetic sequence at the end of the smallest taxonomic unit to which they can be inferred to belong based on character information available in the literature, as discussed below.

**Placement of Unexamined Species.**—*Balmes formosa*. This species is tentatively placed in *Balmes* on the basis of the: (1) reduced number of crossveins in the forewing costal gradate series (New, [1989a]:858, fig. 1) [Character 6], (2) absence an apical hind wing spot (Kuwayama, 1927:123, fig.) [Character 9], and (3) apparent absence of a compact aggregation of modified setae near the insertion of the stylus on the female 9th gonocoxites (New, [1989a]:860, fig. 30) [Character 53]. The *formosa* state of the first character is intermediate between the highly reduced number of costal crossveins found in the three examined *Balmes* species and the much greater number found in most *Psychopsis*. The *formosa* states of the last two characters are plesiomorphic within the Psychopsinae, but their derived states are synapomorphies of the examined species of *Psychopsis*. This species is known only from two specimens cited by Kuwayama (1927) as males, but both of which are probably females (New, [1989a]:846).

*Psychopsis dumigani*, *maculipennis*, and *margarita*. Each of these three species appears to be known only from a small number of female specimens (see their respective Appendix 1 entries). All three species are tentatively placed in the *gracilis* group of *Psychopsis* on the basis of their forewing maculae and fasciae (i.e., Tillyard, 1922a: plate 3 [*dumigani* and *margarita*]; Tillyard, 1925: plate 38, fig. 2 [*maculipennis*]). *Psychopsis maculipennis* clearly ex-

hibits an apical hind wing macula lying posterior to the anastomosis, a synapomorphy of the *gracilis* group [Character 9]; but, in *margarita* the macula is distal to the anastomosis (as in the *insolens* group) and in *dumigani* the macula is diffuse. The large female 8th sternites of *margarita* and *dumigani* (New, [1989a]:870, figs. 116-117; 872, figs. 137-138) are also consistent with their placement in the *gracilis* group.

*Psychopsis gallardi.* The relationships of this spe-

cies remain enigmatic. Although it clearly belongs within the Psychopsinae its relationships with *Balmes* and *Psychopsis* are sufficiently uncertain that I have chosen here not to place it in either genus. Kimmins (1939) placed *gallardi* in *Balmes* based principally on its lack of an apical hind wing macula [Character 9]. However, the absence of this macula is here interpreted as plesiomorphic within the Psychopsinae, and thus cannot support the monophyly of a clade *Balmes* (as interpreted here)
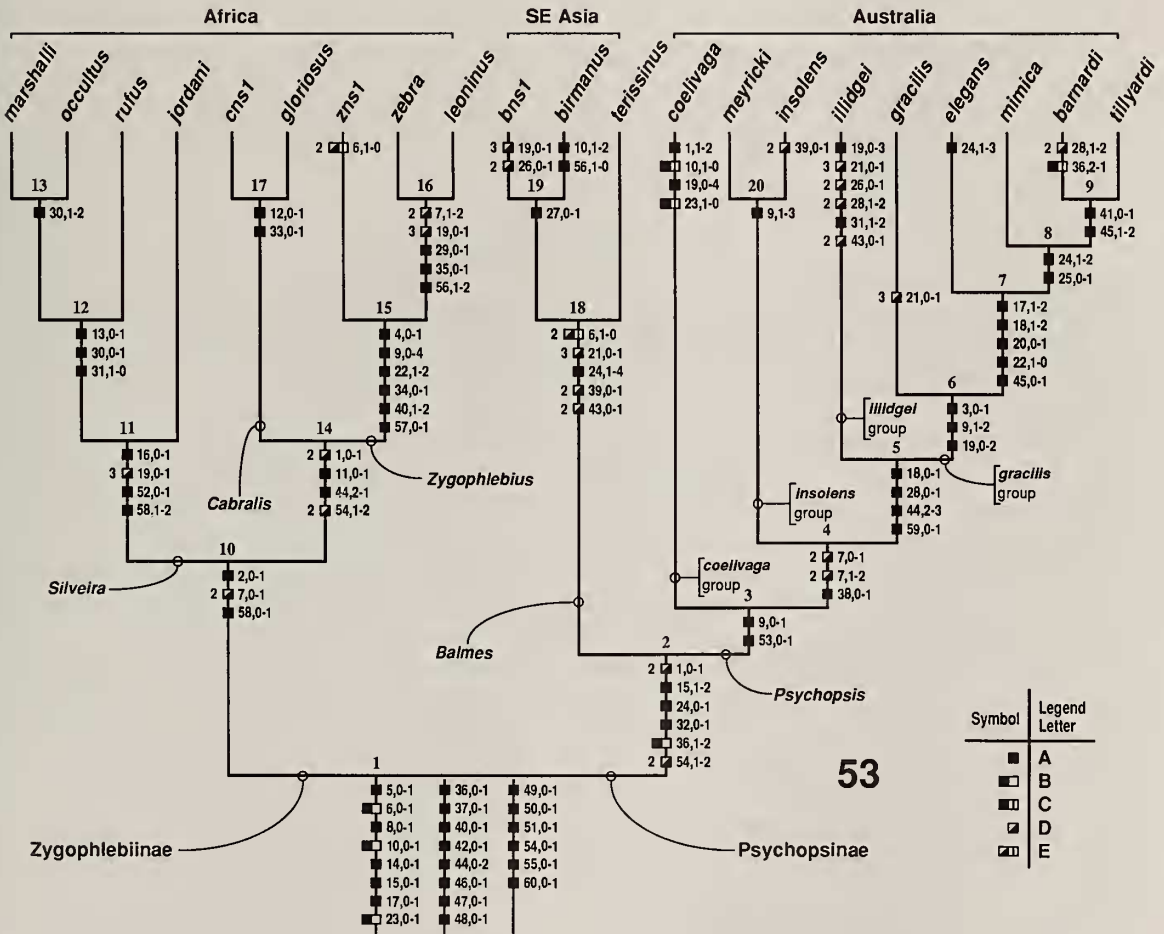


Fig. 53. Cladogram showing the relative relationships among 21 (of 26) living species of silky lacewings (Length = 104, CI = .83, RI = .91). Character state changes are mapped in the following format [left to right]: (1) number of occurrences on the cladogram of the indicated state transformation [if greater than one], (2) lineage symbol, see key below, (3) character number, (4) state numbers [ancestral state - derived state]. LINEAGE SYMBOLS: The relevant transformation is: [A] unique and unreversed, [B] unique but reversed in a distal lineage, [C] unique but a reversal of a basal transformation, [D] a parallelism occurring in two or more lineages, [E] a parallelism and a reversal.

Table 2. Classification of the extant species of the family Psychopsidae. Unexamined species are asterisked.

Family Psychopsidae
    Subfamily Zygophlebiinae
        Genus *Silveira*
            *S. jordani*
            *S. rufus*
            *S. occultus*
            *S. marshalli*
        Genus *Cabralis*
            *C. gloriosus*
            *C. cns1*
        Genus *Zygophlebius*
            *Z. zns1*
            *Z. zebra*
            *Z. leoninus*
    Subfamily Psychopsinae
        Genus *Balmes*
            *B. terissinus*
            *B. birmanus*
            *B. bns1*
            *\*B. formosa*

        Genus *Psychopsis*
            *coelivaga* species group
                *P. coelivaga*
            *insolens* species group
                *P. insolens*
                *P. meyricki*
            *illidgei* species group
                *P. illidgei*
            *gracilis* species group
                *P. gracilis*
                *P. elegans*
                *P. mimica*
                *P. barnardi*
                *P. tillyardi*
                *\*P. dumigani*
                *\*P. maculipennis*
                *\*P. margarita*
         Psychopsinae incertae sedis
                *\*"Psychopsis"* gallardi
                (*Balmes* or *Psychopsis*)

+ *gallardi*. Although the reduced number of forewing costal crossveins [Character 6] (not veinlets) in *gallardi* is a possible *Balmes* synapomorphy, judging from New's ([1989a]:861, figs. 39-40) illustrations of the male terminalia of this species it appears to lack other *Balmes* synapomorphies, i.e., male 9th gonocoxite superprocesses modified into a transverse tumulus [Character 9], microspinose gonosaccus lobes [Character 39], and reduced ventral costae on the male 9th gonocoxites [Character 21]. It also lacks the only identified male synapomorphy which could link it with *Psychopsis*, i.e., an apical hind wing spot [Character 9]. Since females of *gallardi* are unknown, the only other synapomorphy of *Psychopsis* identified here, an aggregation of modified setae near the insertion of the stylus on the female 9th gonocoxites [Character 53], cannot yet be evaluated for this species. Thus, the position of *gallardi* is very uncertain; it may constitute the sister group of either *Balmes* or *Psychopsis*, or both genera. Until further study can be made of both sexes of this species, I believe it prudent to treat *gallardi* as an incertae sedis psychopsine.

**Prior Classifications.**—The six family- and genus-group classifications of extant psychopsids published since 1917 are shown in Tables 3 (worldwide classifications) and 4 (regional classifications).

Navás's (1917) "Ensayo monográfico de la familia de los Sicópsidos" was the first work to comprehensively treat the family Psychopsidae. Earlier works consisted principally of isolated descriptions, but sometimes contained lists of other described species. Navás's revision recognized three tribes with eight genera, 13 species, and three varieties. Taxon characterizations were based solely on venational traits and wing maculation patterns.

Tillyard ([1919a]) revised the Australian psychopsids. Citing overlapping variation in the venational traits used to characterize the four Australian genera recognized by Navás, Tillyard sunk three of Navás' genera, *Artiopteryx* (as *Arteriopteryx* [sic]), *Magallanes*, and *Wernzia*, as synonyms of *Psychopsis*. In the same paper Tillyard erected two new monotypic genera, *Megapsychops* and *Psychopsella* respectively, for the distinctive Australian species *illidgei* and *gallardi*, thus recognizing a total of three Australian genera.

Krüger (1922) reviewed the family based solely on venational characters. He recognized three genera but no subfamilial taxa. Apparently unaware of the works of both Navás (1917) and Tillyard ([1919a]), Krüger placed all southeast Asian and Australian species in a single genus, *Psychopsis*, and proposed two new genera, *Psychophasis* and *Psychomorphe*, to receive the African species. The

latter two genera are, respectively, well-established junior synonyms of the Navásian genera *Silveira* and *Zygophlebius*.

Kimmins' (1939) classification is largely concordant with the earlier scheme of Navás (1917), with the following minor changes: (1) tribal taxa were dropped, (2) Tillyard's *Megapsychops* was recognized, and (3) Tillyard's synonymy of *Artiopteryx* with *Psychopsis* was retained. Again, diagnostic traits at the generic level were restricted to wing maculation and venational characters; however, some interspecific variation in male terminalic characters was noted.

Tjeder (1960) reviewed the African psychopsid fauna. He treated six species, placing them in the same three generic groupings recognized by Navás (1917). This work is also important for its conclusive demonstration of the utility of male and female terminalic characters as diagnostic traits at both the interspecific and intergeneric levels within this family.

New ([1989a]) reviewed the Australian and southeast Asian psychopsid fauna. He, like Tillyard ([1919a]), concluded that considerable intra- and interspecific variation in venational traits mitigated against formal recognition of the several small genera recognized by Navás (1917) in this fauna; however, at the same time he maintained the validity of *Megapsychops,* based primarily on its distinctive forewing venation and patterning. Significantly, New also placed *Balmes* as a synonym of *Psychopsis,* citing overall similarities among the male and female terminalia; however, he also noted the presence of considerable interspecific variation among terminalic structures within his concept of *Psychopsis.*

Two principal character trends are evident from this retrospective appraisal of psychopsid taxonomy. First, terminalic traits have gradually replaced venational traits as the principal source of characters upon which psychopsid classifications are based. This trend, which has paralleled similar shifts in other neuropterous families, is continued in the present work, where 51 of the 60 characters used in the cladistic analysis are male or female terminalic traits. Second, the character base upon which psychopsid classification is founded has diversified over time, and now includes characters from the head, wings (venation and maculation), male terminalia, and female terminalia.

In comparing these prior classifications, if the enigmatic treatment of Krüger is disregarded and the strictly nomenclatural problems caused by differential recognition of the synonymous names *Zygophlebius* and *Notopsychops* are ignored, it is clear that within the African fauna neither the genus-level classification nor the conceptual aggregation of species into genera has undergone much change since the publication of Navás' revision (1917; see Tables 3 and 4). Furthermore, the cladogram derived from the present research (Fig. 53), exhibits a convincing phylogenetic basis for a tripartite division of African psychopsids into the three genera *Silveira, Cabralis,* and *Zygophlebius.*

Thus, the principal taxonomic confusion in the family has revolved around the definition of generic limits within the southeast Asian and, particularly, Australian faunas. The opinions (see Tables 3 and 4) of Navás (1917) and Kimmins (1939) versus Tillyard ([1919a]) and New ([1989a]) differ considerably with regard to generic limits. However, surprisingly, both of these seemingly divergent viewpoints are reflected in the cladogenetic relationships inferred here among the species of these faunas.

Based on the cladogeny proposed here (Fig. 53), the genera *Balmes* (southeastern Asia) and *Psychopsis* (Australia) constitute sister-groups within the subfamily Psychopsinae. However, the three most basal lineages within *Psychopsis* correspond closely to the earlier genera *Wernzia* (type species: *coelivaga*), *Magallanes* (type species: *insolens*), and *Megapsychops* (type species: *illidgei*). Thus, an alternative fully sequenced classification based on this cladogram might recognize five genera within the Psychopsinae: *Balmes, Wernzia, Magallanes, Megapsychops,* and *Psychopsis* s.str. Such a classification would correspond closely to those proposed by Navás (1917) and Kimmins (1939).

However, I believe that a two-genus division of the Psychopsinae is preferable for three reasons: (1) the biogeographic cohesiveness of generic taxa, (2) concern about the proliferation of monotypic genera, and (3) the uncertain phylogenetic position of *gallardi.* First, the proposed bipartite division of the Psychopsinae has the advantage of restricting the apparent distribution of monophyletic psychopsid clades to discrete continents, i.e., the subfamily Zygophlebiinae to Africa, *Balmes* to southeastern Asia, and *Psychopsis* to Australia. Second, recognition of five, rather than two, psychopsine genera would require the recognition of two monotypic genera, *Wernzia* (for *coelivaga*) and *Megapsychops* (for *illidgei*), and a third genus, *Magallanes,* with

Table 3. Worldwide psychopsid classifications (1917-present). Spellings of names have been corrected where necessary. Synonymous generic names are placed collinearly.

| Author & Year | Navás 1917 | Krüger 1922 | Kimmins 1939 |
|---|---|---|---|
| African Taxa | Zygophlebini | — | — |
| | *Silveira* | *Psychophasis* | *Silveira* |
| | *Cabralis* | — | *Cabralis* |
| | *Zygophlebius* | *Psychomorphe* | *Notopsychops* |
| Australian & Oriental Taxa | Balmesini | — | — |
| | *Balmes* | — | *Balmes* |
| | Psychopsini | — | — |
| | *Wernzia* | — | *Wernzia* |
| | *Magallanes* | — | *Magallanes* |
| | — | — | *Megapsychops* |
| | *Artiopteryx* | — | — |
| | *Psychopsis* | *Psychopsis* | *Psychopsis* |

Table 4. Regional psychopsid classifications (1919-present). Spellings of names have been corrected where necessary.

| Author & Year | Tillyard [1919a] | Tjeder 1960 | New [1989a] |
|---|---|---|---|
| African Taxa | — | *Silveira* | — |
| | — | *Cabralis* | — |
| | — | *Notopsychops* | — |
| Australian & Oriental Taxa | *Psychopsella* | — | — |
| | *Megapsychops* | — | *Megapsychops* |
| | *Psychopsis* | — | *Psychopsis* |

only two species (*meyricki* and *insolens*). In my opinion, there is no compelling reason to encumber the literature with this arrangement. Third, as noted above, the species *gallardi* is currently known only from one sex (male), and its true phylogenetic position within the Psychopsinae is unknown. Under a two-genus division of the Psychopsinae this species (when its affinities become known) could easily be incorporated into either *Balmes* or *Psychopsis* as a sister lineage without requiring a nomenclatural change. However, if *gallardi* is found to constitute the sister-group of a clade (*Wernzia* + (*Magallanes* + (*Megapsychops* + *Psychopsis* s.str.))) under the five-genus system, yet another monotypic genus (*Psychopsella*, type species: *gallardi*) would be required to incorporate this species into a sequenced classification of the family.

Finally, it should be noted that if a broad concept of *Psychopsis* is to be adopted, the species *illidgei* cannot also be accorded generic rank (e.g., as proposed by New [1989a]) without compromising the monophyly of *Psychopsis*. According to the classificatory division of the cladogram adopted here, *illidgei* is simply a highly autapomorphic species of *Psychopsis*.

## BIOGEOGRAPHIC ANALYSIS

### INTRODUCTION

The distribution of extant psychopsids is distinctly tripartite (Fig. 54). The genus *Psychopsis* is endemic to Australia; *Balmes* is restricted to southeast Asia (mainland and Taiwan); and *Silveira*, *Cabralis*, and *Zygophlebius* are endemic to the southern half of Africa. All available distributional data

suggest that the taxa occupying these three areas are completely disjunct. No living silky lacewings are known from any of the intervening and/or adjacent areas of northern Africa, Madagascar, the Middle East, India, the Malay Archipelago, or New Guinea.

The fossil genera currently attributed to the family Psychopsidae are listed in Table 5. The extinct families Kalligrammatidae, Brong-niartiellidae, and Osmylopsychopsidae contain a number of additional taxa thought to be closely related to psychopsids. Unfortunately, the less than optimal preservation of most 'psychopsoid' fossils limits observations of some critical character suites, particularly terminalia; this, together with the in-adequacy of revisionary and phylogenetic studies of fossil 'psychopsoids,' currently prohibits critical evaluation of relationships among extant and fos-sil 'psychopsoid' taxa. Consequently, it is prema-ture to attempt to fully combine distributional data from recent and fossil psychopsids into a compre-hensive hypothesis of silky lacewing biogeogra-phy. However, assuming that the genera in Table 5 are correctly placed in the family Psychopsidae, several preliminary conclusions appear justifiable. First, the presence of psychopsids on both Laurasia (e.g., Germany, Kazakhstan, China) and Gondwanaland (Australia) during the Mesozoic supports the idea that silky lacewings were widely distributed during this era. Second, the 11 de-scribed genera of fossil psychopsids (with ca. 15 species) suggest that silky lacewings were mor-phologically diverse as well as geographically wide-spread during the Mesozoic, with their principal radiation possibly occurring during the Jurassic. Third, the oldest fossils attributed to the
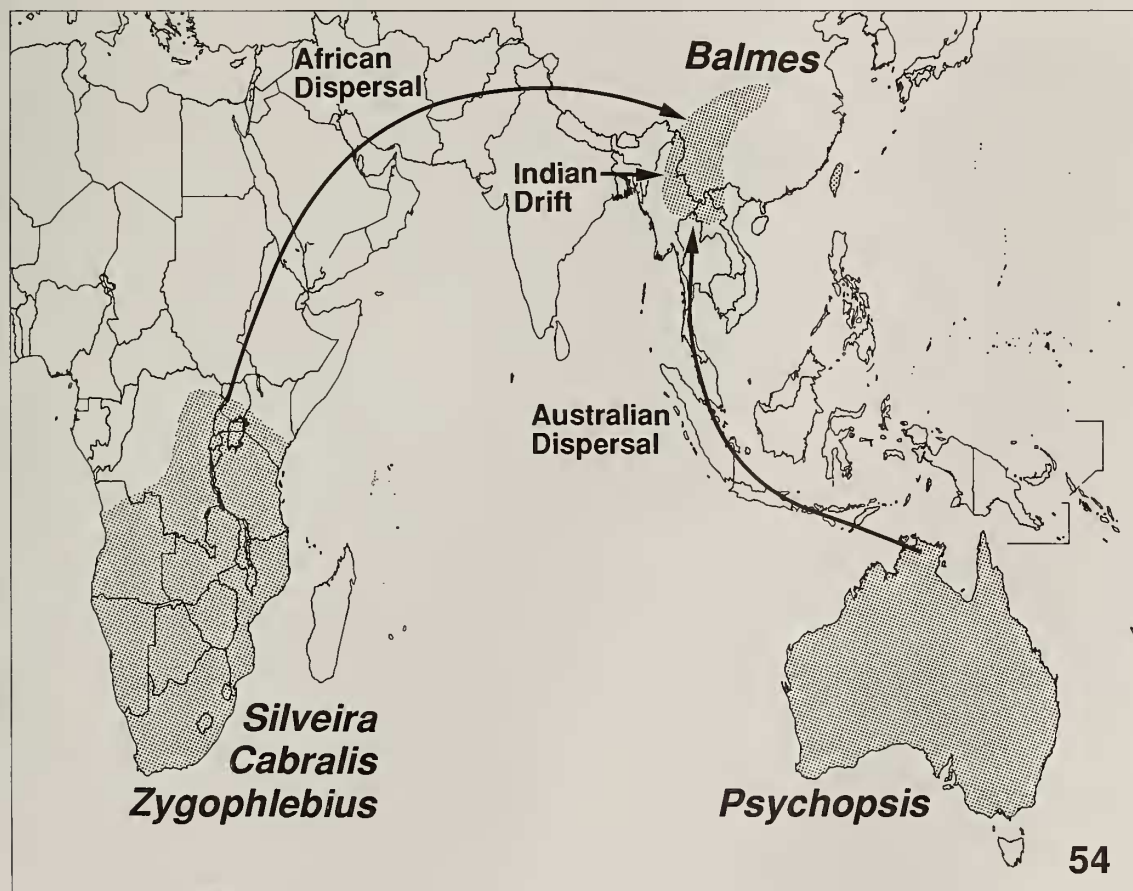


Fig. 54. World distribution of extant psychopsids (equal area map projection). The ranges of the south African genera *Silveira, Cabralis,* and *Zygophlebius* have been combined. *Psychopsis* records from western, particularly northwestern, Australia are sparse. The limits of the range of *Balmes* in southeastern Asia are imprecisely known.

Table 5. Fossil genera of the family Psychopsidae.

| Genus | Temporal Distribution | Geographic Distribution |
|---|---|---|
| *Miopsychopsis* Makarkin, 1991 | Miocene | USSR |
| *Propsychopsis* Krüger, 1923 | Oligocene | Europe, N. Am. |
| *Embaneura* Zalessky, 1953 | Cretaceous | USSR |
| *Grammapsychops* Martynova, 1954 | Cretaceous | USSR |
| *Angaropsychops* Martynova, 1949 | Upper Jurassic | USSR |
| *Calopsychops* Panfilov, 1980 | Upper Jurassic | Kazakhstan |
| *Propsychops* Panfilov, 1980 | Upper Jurassic | Kazakhstan |
| *Beipiaopsychops* Hong, 1983 | Middle Jurassic | China |
| *Sinopsychops* Hong, 1982 | Middle Jurassic | China |
| *Apeirophlebia* Handlirsch, [1906] | Upper Lias | Germany |
| *Triassopsychops* Tillyard, 1922b | Upper Triassic | Australia |

Psychopsidae (Upper Triassic of Australia) date the origin of the family prior to the division of Pangea into Laurasia and Gondwanaland. Fourth, the presence of psychopsids on Laurasian land areas (North America: Florissant, CO; Europe: Baltic amber) during the Tertiary suggests that the disappearance of silky lacewings from much or most of ancient Laurasia is a relatively recent event.

Tillyard ([1919a]:764) suggested a Gondwanan origin for the family Psychopsidae based on his knowledge of (1) the tripartite distribution of living species and (2) apparently closely related fossil taxa in the families Kalligrammatidae and Prohemerobiidae, which were then known from Mesozoic strata in Australia and Europe. This view was reiterated without additional support by New ([1989a]:841). Neither Tillyard nor New commented specifically on the biogeographic significance of the occurrence of psychopsids on apparently Laurasian areas of southeast Asia, which is anomalous under the Gondwanan origin hypothesis. Presumably, both would have explained this occurrence by postulating the dispersal of a Gondwanan ancestor from Australia across the Malay Archipelago to mainland Asia. While such a proposal would be consistent with both their hypothesis and the observed distributions of extant psychopsids, several other plausible biogeographic hypotheses can be marshalled to explain the presence of silky lacewings in southeast Asia. Below, I outline four such hypotheses, develop a method for discriminating among them, and use the method to show that one hypotheses is better supported by the available data than the other three.

## BIOGEOGRAPHIC HYPOTHESES

The four biogeographic hypotheses outlined below have been developed from a simple model of the tectonic fragmentation of Pangea, and the subsequent interactions of Laurasia with fragments of Gondwanaland. Rosen (1978:185, fig. 24) illustrated the relative relationships among most of the major tectonic fragments of Pangea. This illustration is reproduced in Fig. 55, and reduced to the land areas occupied by extant psychopsids in Fig. 56. Given the land area relationships shown in the latter figure, at least four different histories of landmass occupancy (Figs. 57, 59, 61, 63) are possible for an ancestral lineage leading to extant southeast Asian psychopsids. These histories constitute four different biogeographic explanations (hypotheses) that could account for the current presence of psychopsids in southeast Asia. Each of the hypotheses assumes that the stem ancestor of the Psychopsidae (1) occupied some portion of Pangea and (2) predated the division of Pangea into Laurasia and Gondwanaland. The validity of these assumptions is supported by the existence of the psychopsid fossil *Triassopsychops* from the Upper Triassic of Australia.

*Laurasian Relic Hypothesis* (Fig. 57): The Laurasian Relic hypothesis interprets southeast Asian psychopsids as the descendents of an ancient Laurasian (rather than Gondwanan) ancestor. Several psychopsid fossils have been reported from Laurasian land areas (i.e., Europe [Baltic Amber] and North America) during the Tertiary, far postdating the division of Laurasia and Gondwanaland.

Although not numerous, these fossils document a wide distribution of psychopsids on Laurasian land areas until relatively recent times, and confirm the plausibility of deriving southeast Asian psychopsids from Laurasian rather than Gondwanan ancestors.

*Indian Drift Hypothesis* (Fig. 59): The Indian Drift hypothesis interprets southeast Asian psychopsids as the descendents of Gondwanan ancestors that drifted northward on the Indian Plate and were introduced onto Eurasia as a consequence of the conjunction of India and Eurasia in the early Eocene (Brown & Gibson, 1983). Although no recent or fossil psychopsids are known from Indian Plate land areas, the plausibility of this hypothesis is suggested by the close proximity of the known western limit of the range of *Balmes* (i.e., Burma, south central China) to the eastern margin of this plate (Fig. 54).

*Australian Dispersal Hypothesis* (Fig. 61): The Australian Dispersal hypothesis interprets southeast Asian psychopsids as the descendents of ancestors that dispersed northwesterly from Australia through the Malay Archipelago to mainland Asia. The plausibility of this hypothesis derives primarily from the existence of a readily apparent dispersal route, i.e., the islands of Malesia, from Australia to southeast Asia. Detracting evidence includes the absence of any records of extant and/or fossil psychopsids from any land areas along this possible dispersal route.

*African Dispersal Hypothesis* (Fig. 63): The African Dispersal hypothesis interprets southeast Asian psychopsids as the descendents of ancestors that dispersed to southeast Asia from Africa. Dispersal could have occurred by at least two routes: (1) direct transoceanic dispersal, which seems unlikely given the limited flight capabilities of psychopsids and the extreme distance separating southern Africa and southeast Asia throughout the Cenozoic and Mesozoic eras, or (2) transcontinental dispersal northward through Africa to the Middle East, then eastward to southeast Asia. The principal detracting evidence of the latter route is the absence of any known remnant populations of extant psychopsids along this path.

## HYPOTHESIS TESTING

The conceptual development of area-cladograms and their application to biogeographic studies has been an important recent development in cladistic theory (Nelson & Platnick, 1981; Humphries & Parenti, 1986). Area-cladograms are cladograms depicting hypotheses of relationships among geographic areas and are generally produced by the substitution of the terminal taxa of a calculated taxon-cladogram by their respective distributions. However, given a set of known area relationships and a biogeographic hypothesis consistent with those relationships, it is also possible to predict the form of the area-cladogram corresponding to the biogeographic hypothesis. This characteristic can be exploited to divide a large set of plausible biogeographic hypotheses into several smaller sets, each of which predicts a different area-cladogram. By matching the actual area cladogram of a test taxon to one of the sets of predicted area-cladograms, a reduced field of biogeographic hypotheses can be identified that are consistent with (1) the test taxon cladogeny, (2) the test taxon geographic distribution, and (3) the underlying known area relationships.

In the present case, the area relationships between southeast Asia (assumed here to be part of Laurasia, but see below), Africa, and Australia (Fig. 56) are well supported by the known fragmentation sequence of Pangea and Gondwanaland (Rosen, 1978, Smith et al., 1981). The landmass occupancy histories required by the ancestors of southeast Asian psychopsids under each of the four biogeographic hypotheses listed above are given in Figs. 57, 59, 61, and 63 (narrow lines and underlined land areas), where they are mapped on replicas of Fig. 56 to show their consistency with the area relationships there depicted. The corresponding predicted area cladograms are shown in Figs. 58, 60, 62, and 64. Note that the first three hypotheses predict different area cladograms but that the Indian Drift and African Dispersal hypotheses predict the same area cladogram (and thus are not separable by this method). A finding of the latter area cladogram in the test taxon would, however, still contain information by excluding the Laurasian Relic and Australian Dispersal hypotheses.

The derivation of the area cladogram predicted by the Indian Drift hypothesis is explained below as an example of the logic of deriving predicted area cladograms from landmass occupancy histories. Note that under the Indian Drift hypothesis (Fig. 59) the ancestors of southeast Asian and African taxa are predicted to share a more recent common ancestor (on Afroindia) than either does with
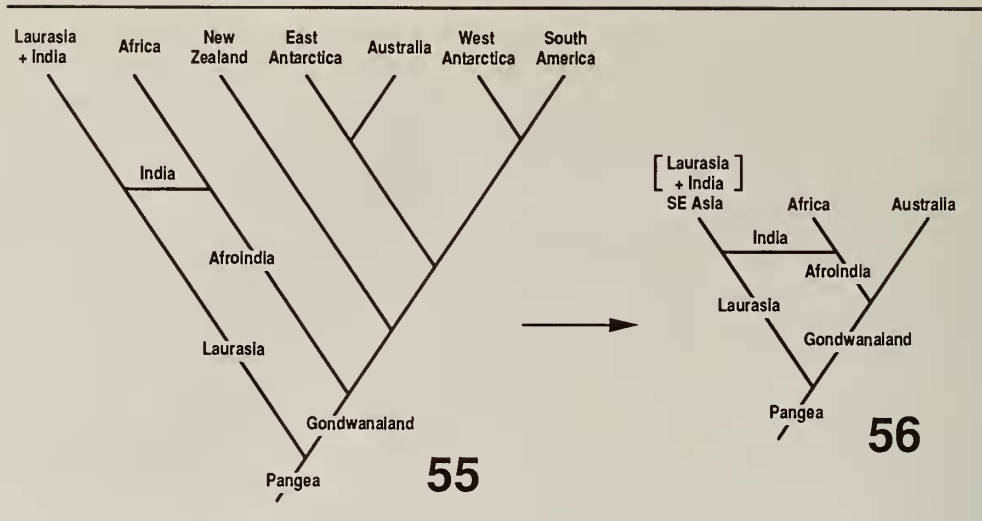
Figs. 55-56. 55. Cladistic representation of the relative relationships between selected landmasses stemming from the tectonic fragmentation of Pangea (redrawn from Rosen 1978:185, fig. 24). 56. Cladistic representation of the relative relationships between the land areas occupied by living psychopsids (reduced from Fig. 55).

Australian taxa. This is reflected in the predicted area cladogram (Fig. 60) by assigning "SE Asia" and "Africa" to the terminal bifurcation of the area cladogram, and joining "Australia" basally.

### RESULTS

The actual area-cladogram found for extant psychopsids (Fig. 53) matches the area-cladogram predicted by the Australian Dispersal hypothesis (Fig. 62).

### DISCUSSION

The results support the contention that southeast Asian psychopsids reached mainland Asia via dispersal from Australia through the Malay Archipelago, and are inconsistent with the alternative hypotheses that they (1) represent a relic of a long-endemic fauna of Laurasian ancestry [Laurasian Relic], (2) dispersed from Africa via the Middle East [African Dispersal], or (3) dispersed from Gondwanaland via the Indian Plate [Indian Drift]. The Australian Dispersal hypothesis is also consistent with the following overall biogeographic hypothesis for extant psychopsids: (1) the most recent common ancestor of extant psychopsids inhabited some portion of Gondwanaland, (2) extant psychopsid taxa occupying Australia and sub-Saharan Africa represent endemic elements which differentiated in-place subsequent to the rifting of Africa from the remainder of Gondwanaland [in-

cluding Australia], and (3) the occupation of mainland Asia by ancestors of the genus *Balmes*, derived from an ancient Australian taxon, is a more recent event. This scenario also accords with Tillyard's ([1919a]) general suggestion of a Gondwanan origin for the family Psychopsidae.

The support found here for a dispersalist explanation of the occurrence of *Balmes* in southeast Asia depends importantly on the structure of the limited tectonic model of Gondwanan fragmentation employed here. This model, and the area-cladograms predicted by the four evaluated biogeographic hypotheses based on it, provides a means of assessing the relative plausibility of the different hypotheses. Alteration of the underlying model, however, could (1) shift support to an alternative hypotheses predicting a different area-cladogram, or (2) fail to produce unambiguous results where multiple biogeographic hypotheses predict identical area-cladograms.

The second possibility is apparent in the present model where the area-cladograms predicted by the Indian Drift and African Dispersal hypotheses are identical. A similar and more interesting result based on a slightly altered tectonic model is discussed below. Audley-Charles (1987) summarized geological evidence for the hypothesis that Burma, the Malay peninsula, and Sumatra (together with several other islands of the Malay Archipelago) represent terranes which rifted off the northern margin of Gondwanaland, adjacent to present-day
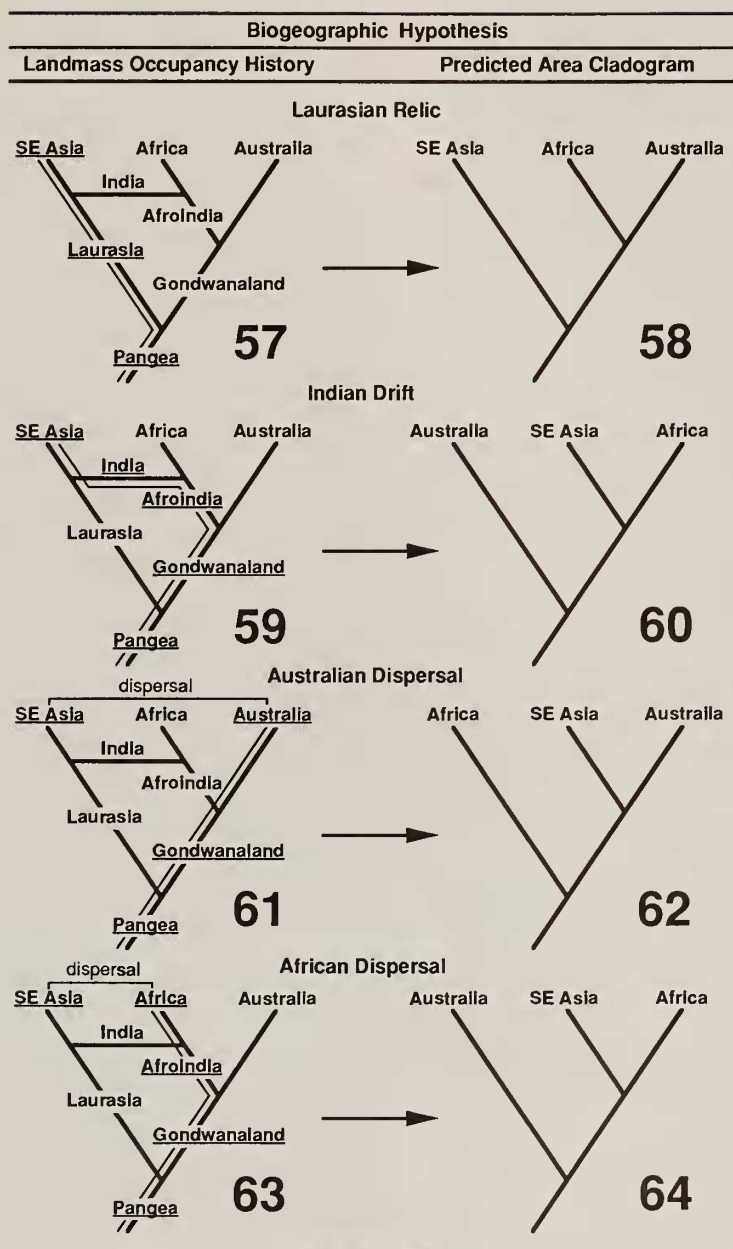
Figs. 57-64. Landmass occupancy histories and their corresponding predicted area cladograms for four biogeographic hypotheses which could account for the presence of living silky lacewings in southeast Asia. Each landmass occupancy history traces (narrow line) the inferred sequence of landmasses (underlined) which must have been occupied by the lineal ancestors of living southeast Asian psychopsids under a particular biogeographic hypothesis, given the relative relationships between land areas shown in Fig. 56. The corresponding predicted area cladograms show the areal relationships expected from a cladistic analysis of a higher taxon occupying each of the three terminal areas.

northern Australia, and subsequently accreted to Eurasia. These terranes, at least some of which were probably above water during the late Mesozoic and early Tertiary, provide another possible vehicle for the introduction of ancestral, Gondwanan, psychopsids into southeast Asia. On the area-cladogram shown in Fig. 56, such terranes would be represented by one or more lines arising from the Australian stem after its divergence from Afroindia. It should be noted that under this augmented model of Gondwanan fragmentation a simple comparison of actual to predicted psychopsid area-cladograms cannot differentiate between the Australian Dispersal hypothesis and the alternative hypothesis that the ancestors of southeast Asian psychopsids reached Eurasia vicariantly by drifting northward on such a terrane, because both hypotheses (1) predict the same area-cladogram (Fig. 62) and (2) match the actual area-cladogram (Fig. 53).

In conclusion, while the comparison of a calculated (actual) area-cladogram with area-cladograms predicted from a set of biogeographic hypotheses consistent with the known relationships among a suite of areas can be powerful tool for restricting the number of plausible biogeographic hypotheses, it does not guarantee identification of a unique "best" hypothesis. However, even with the latter shortcoming, this method has the potential to contribute significantly to our understanding of the biogeography of individual taxa occurring in the biotically complex region of southeast Asia because of its ability to discriminate between at least three important classes of relevant biotic elements: (1) ancient Laurasian endemics, (2) rafted or non-rafted Australian immigrants, and (3) African or rafted Indian immigrants.

## SUGGESTIONS FOR FUTURE RESEARCH

**Phylogeny.**—Future work on psychopsid phylogeny should concentrate on (1) assessing the phylogenetic position of the Psychopsidae within the Neuroptera, i.e., its interfamilial relationships, and (2) testing the intrafamilial relationships proposed here by including in subsequent analyses both new taxa (i.e., fossil species and the five extant species not examined here) and new character data (e.g., from molecules, preimaginal morphology, and fossils). Investigations of phylogenetic relationships between living and fossil psychopsids would be of particular interest because of their relevance to the biogeography of the family. Among the extant species, the position of the incertae sedis species "*Psychopsis*" *gallardi* is of special interest.

**Taxonomy.**—Although few species of Recent psychopsids probably remain to be discovered, some additional taxonomic work is still needed. Two priorities in this area are (1) the completion of a revisionary study of the genus *Balmes* and (2) the discovery, description, and comparative analysis of the preimaginal stages of psychopsid species. In the latter area, the rearing of larvae should be emphasized to ensure positive species identifications. Comparative studies of heterospecific and/or heterogeneric larvae are especially needed to further the ends of taxonomic identification, phylogenetic inference, and the study of functional morphology.

**Ecology and Natural History.**—Studies of the ecology and natural history of all psychopsid species are needed. Little more than anecdotal information exists in either of these areas for any species. Field studies containing detailed information on topics such as microhabitat and feeding preferences, abundance, spatial distribution, movement patterns, behavior, longevity, etc. are conspicuously lacking in the literature. This statement applies equally to both larvae and adults. Of special interest would be the verification or refutation of the hypotheses advanced above for psychopsid copulation and oviposition, particularly those regarding in-flight egg deposition. Individuals who conduct field studies should be careful to deposit selected specimens, especially reared larvae, in an established public collection where they can be made available to future researchers for comparative study. The existence of such deposits should be published in some appropriate manner.

**Fossils.**—The number of fossil genera attributed to the Psychopsidae has nearly doubled during the last 15 years. A comprehensive comparative revision of these taxa is now needed. Such a work could contribute significantly to our knowledge of psychopsid phylogeny and biogeography.

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APPENDIX 1

Synonymical Catalog of Extant Psychopsids
APPENDIX 1

## Synonymical Catalog of Extant Psychopsids and Material Examined

To augment the family- and genus-level taxonomic data contained in the main text, a synonymical catalog of extant psychopsid species is presented below. Each species treatment contains a concise distributional statement, a synonymical listing with annotated bibliographic citations, a flight period statement, and a listing of material examined. Distribution statements reflect geographic data associated with examined specimens and records cited in Tjeder (1960) and New ([1989a]). Binomina enclosed in brackets in the synonymical listings indicate incorrect determinations. "FLIGHT PERIOD" statements give extreme capture dates; except where otherwise indicated, cited data reflect only temporal data associated with examined specimens. "MATERIAL EXAMINED" statements present selected label data in the format: COUNTRY: POLITICAL SUBDIVISION: # males, # females, # sex undeterminable ["?"; e.g., abdominal apex missing], geographical collection data, temporal collection data, miscellaneous data, collector(s) surname(s) (REPOSITORY COLLECTION ACRONYM). Material in brackets has been added for clarity. Collection acronyms are expanded above under the heading "Materials and Methods: Collection Acronyms." An asterisk (*) following an annotation indicates a figure (e.g., forewing* = forewing figure). Taxa are listed in the order shown in Table 2.

Family PSYCHOPSIDAE Handlirsch
Subfamily ZYGOPHLEBIINAE Navás
Genus **SILVEIRA** Navás

**jordani** Kimmins, 1939: southwestern Africa
*Silveira jordani* Kimmins, 1939:148 [original description, male terminalia*, wing*].—Tjeder, 1960 [redescription, distribution, male terminalia*, female terminalia*, wing*, habitus*].
FLIGHT PERIOD: 21 September - 16 April [Outlier: June (day unrecorded), see Tjeder, 1960:191]. MATERIAL EXAMINED [12M, 3F, 1? = 16]: **NAMIBIA**: 3M, Homeb. Namib National Park, 23.i.1988, Miller & Stange (FSCA); 2M, 1F, Namib/Naukluft Park, Gobabeb, 23°34'S, 15°03'E, 18.ii-7.iii.1983, ex. Malaise trap, Mansell (NCIP); 1F, Namib/Naukluft Park, Kuiseb R. nr. Gobabeb, 23°34'S, 15°03'E, 18.ii-20.iii.1983, ex. light, Kuiseb Survey (NCIP); 1M, TSES, S[outh] W[est] A[frica], 1924, Brown (SAMC); 1?, 7 mi. S. Ombika, Etosha Pan, 27.x.1967, 1150m, Ross & Stephen (CAS); 1M, Gobabeb, Namib Desert Research Station, 12.x.1967, 407m, Ross & Stephen (CAS); 2M, Blässkranz 7, 24°06.5'S, 16°14.5'E, Maltahöhe Dist., 12-14.x.1984, Irish (SMWW); 1M, Orange River, 28°02'S, 17°04'E, Lüderitz District, 15-16.iv.1986, Irish (SMWW); 1M, Anikamkarab, 2.ii.[19]69 (SMWW). **SOUTH AFRICA: CAPE PROVINCE:** 1M, Clanwilliam, 30.i.1983, Stange & Miller (FSCA); 1F, Cape, Namaqualand, Worden[w?], 21.ix?.[18]86 (SAMC).

**rufus** Tjeder, 1960: southeastern Africa
*Silveira rufa* [sic] Tjeder, 1960:185 [original description, male terminalia*, female terminalia*, wing*, habitus*].
FLIGHT PERIOD: 4 November (see Tjeder, 1960:188) - 26 February [Outlier: 10 July, see Tjeder, 1960:188]. MATERIAL EXAMINED [2M]: **SOUTH AFRICA: TRANSVAAL:** 1M,

D'Nyala Nat. Res., Ellisras District, 23°45'S, 27°49'E, 23-26.ii.1987, Mansell (NCIP); 1M, Potgi[l?]eters Rust, xii.1919, Malla (SAMC).

**occultus** Tjeder, 1960: southwestern Africa

*Silveira occulta* [sic] Tjeder, 1960:180 [original description, male terminalia*, female terminalia*, wing*, habitus*].

FLIGHT PERIOD: 22 February - 26 May. MATERIAL EXAMINED [9M, 39F, 3? = 51]: **ANGOLA:** 22F, 20km NE Sa da Bandeira, 4.iii.[19]70, 5600', Ross (CAS); 1F, 18 mi. N. Chicuma, 26.v.[19]58, 1200m, Ross & Leech (CAS). **ANGOLA or NAMIBIA:** 1?, Erikson's Drift, Kunene R[iver], iii.1923, S. W. Africa Mus. Exped. (SAMC). **NAMIBIA:** 3M, 1F, 1?, Deutsch SW. Afrika (ZMHB); 1M, 1F, D.SW. Afrika, Okahandya, 25.iv.[19]02?, Schultze (ZMHB); 1M, 2F, Elefantenberg, Farm Achalm, 9km S. Otavi, 19°44'S, 17°21'E, 12.iii.1987, Oberprieler (NCIP); 1F, Windhoek, SE 2217 Ca, 13.iii.1971 (SMWW); 1F, Damaraland, Sebraskop 410, 20°44'S, 15°09'E, 13.iv.1987, Irish & Marais (SMWW); 2F, Otjitambi, "1970," 29.iii.[19]51 (SMWW, UZIL); 1M, Windhuk [=Windhoek], Zobrys (UZIL); 3M, 2F, Okahandja, iii.1969, 18.ii.1958 [paratype, Gaerdes], 10.iii.1958 ["allotype," Gaerdes], 22.ii.[19]36 [paratype], 21.iii.[19]56 [paratype] (SMWW, UZIL); 6F, Okahandja, 2116DD, 13-14.iii.1969, Lamoral & Day (UZIL). **COUNTRY UNCERTAIN:** 1?, "Guinea," P. Andongo, 27.v.[18]75, Homeyer (ZMHB).

**marshalli** (McLachlan, 1902): southeastern Africa

*Psychopsis marshalli* McLachlan, 1902:234 [original description].

*Psychopsis nebulosa* Van der Weele, 1907:146 [original description, male terminalia*].

*Silveira marmoratus* Navás, 1912b:196 [original description].—Navás, 1917 [redescription]; Navás, 1928 [distribution].

*Zygophlebius nebulosa* [sic].—Navás, 1917 [redescription, distribution].

*Psychophasis marshalli*.—Krüger, 1922 [listed].

*Silveira marshalli*.—Kimmins, 1939 [listed, distribution, wing*]; Tjeder, 1960 [redescription, distribution, male terminalia*, female terminalia*, wing*, habitus*].

FLIGHT PERIOD: 3 November - 7 April [Outlier: July (day unrecorded), see Tjeder, 1960:180]. MATERIAL EXAMINED [27M, 39F, 6? = 72]: **BOTSWANA:** 1M, 1F, Serowe, i.1990, ex. Mal-aise trap, Forchhammer (CAS); 4M, 1F, Serowe, Farmer's Brigade, ii.1988, ex. Malaise trap, Forchhammer (USNM); 1M, Ngoma, 24.ii.1980, Owen (NMK). **SOUTH AFRICA: TRANSVAAL:** 1?, Ost-Transvaal, Karino, iii.1911, Cooke (ZMHB); 1F, 5mi. W Warmbad, 24-25.ii.1968, Krombein & Spangler (USNM); 1M, Kruger Nat. Park, Olifants Camp, 19.ii.1968, Krombein & Spangler (USNM); 5M, 2mi. N Messina, 24.iii.[19]58, 590m, Ross & Leech (CAS); 1F, Nylstroom, 24°42'S, 28°20'E, 30.xi.1970, Schalkwyk (NCIP); 1M, 5F, 12km N Nylsspruit, 16.ii.1983, Miller (FSCA, CUIC); 1M, Messina, 11.ii.1985, ex. light, Aspöck, Hölzel & Mansell (NCIP); 1M, 1F, Langjan Nature Res. 22°52'S, 29°14'E, 2.ii.1984, ex. light, Mansell (NCIP). **ZAIRE:** 1? (tentative identification), 150-200mi. W. Kambove [=?Kambove at 10°52'S, 26°38'E], 3.xi.[19]07, 3500-4500ft., Neave? (BMNH). **ZIMBABWE (=S. RHODESIA):** 9M, 18F, 5mi. S Lupani, 11.ii.1970, 3000ft, Ross (CAS); 3F, 41mi. S Umtali, 17.iii.[19]58, 640m, Ross & Leech (CAS); 1F, 3mi. E Matapo Mission (=? in Matopo Hills), 14.ii.1970, 5000ft, Ross (CAS); 1F, Bikita Mines, 19.iii.[19]58, 1200m, Ross & Leech (CAS); 1M, 10mi. NE Filabusi, 21.iii.[19]58, 1100m, Ross & Leech (CAS); 1F, 33mi. SE Chirundu, 8.iii.[19]58, 1170m, Ross & Leech (CAS); 1F, Khami Ruins, 14mi. W Bulawayo, 22.iii.[19]58, 1275m, Ross & Leech (CAS); 1F, Guelo, 7.iv.1917, Skaife (SAMC); 2M, 3F, 4?, Salisbury, 7.i.[19]15, 17.ii.[19]15, 7.i.[19]17, iii.[19]18, 22.ii.[19]19, 10.ii.[19]20, +3 without date, various coll. (SAMC, NMK, USNM).

## Genus **CABRALIS** Navás

**gloriosus** Navás, 1912: southeastern Africa

*Cabralis gloriosus* Navás, 1912a:110 [original description, wing*].—Navás, 1917 [redescription, distribution]; Navás, 1931 [listed, distribution]; Kimmins, 1939 [listed, distribution]; Tjeder, 1960 [redescription, distribution, male terminalia*, female terminalia*, wing*, habitus*].

FLIGHT PERIOD: 19 November - 15 February. MATERIAL EXAMINED [13M, 6F = 19]: **SOUTH AFRICA: TRANSVAAL:** 1M, 2F, Ingwe, 10 km N. Louise Trichardt Hotel, 15.ii.1988, Miller (FSCA); 3M, Louis Trichardt district, 22°58'S, 29°56'E, 3.ii.1990, ex. dense brush along stream, Minter (MINTER); 2F, Louise Trichardt, Hanglip, Ingwe, 23°00'S,

29°57′E, 10.ii.1985, ex. forest, Minter (MINTER); 4M, 1F, Wylliespoort, Ingwe Motel, 22°58′S, 29°57′E, 19.xi/30-31.i.1984, Mansell (NCIP). **ZIMBABWE (=S. Rhodesia):** 3M, 1F, Burma Valley, Mutare district, 19°12′S, 32°42′E, 19.xi.1990, netted in forest, Minter (MINTER); 1M, Burmah Valley, Umtali, xi.1953, Pinhey (NMK); 1M, Umtali, 20.i.[19]48, Pinhey (NMK).

**cns1** (=*Cabralis* new species #1; undescribed): west central Africa

FLIGHT PERIOD: 18 October - December (day unrecorded). MATERIAL EXAMINED [12M, 7F, 2? = 21]: **ZAIRE (=Belgian Congo):** 2M, 4F, 1?, Lulua: Kapanga [8°21′S, 22°35′E], 11.xi.1932, x.1933 (MRAC [papered]); 9M, 2F, 1?, Lulua: Riv. Luiza [ca. 7°35′S, 22°40′E], 18.x.1933, x.1933, Overlaet (MRAC [papered]); 1F, Sandoa [9°41′S, 22°52′E], xii.1931 (MRAC); 1M, Tshibaba [=?7°55′S, 22°24′E], 14.xi.193[2?] (MRAC [papered]).

## Genus ZYGOPHLEBIUS Navás

**zns1** (=*Zygophlebius* new species #1; undescribed): southeastern Africa

FLIGHT PERIOD: Unknown. MATERIAL EXAMINED [2M, 2F = 4]: **SOUTH AFRICA: TRANSVAAL:** 2M, 2F, Chuenespoort [=Chuniespoort, 24°16′S, 29°33′E] area, S of Pietersburg, no date, Minter (MINTER).

**zebra** (Brauer, 1889): southeastern Kenya and adjacent Tanzania [not Madagascar, see Tjeder, 1960:198] (Notes: Many early literature records for "*zebra*" actually pertain to "*leoninus*." The specific name "*zebra*" is treated here as a noun in apposition, Art. 31b(ii).).

*Psychopsis zebra* Brauer, 1889: 102 [original description].—Kolbe, 1897 [redescription, distribution]; Van der Weele, 1907 [distribution, male terminalia*]; Van der Weele, 1909 [listed, distribution]; Navás, 1914 [listed, distribution]; Fraser, 1951 [listed, distribution].

*Zygophlebius zebra* [var. *zebra*?].—Navás, 1917 [redescription, distribution].

*Psychomorphe zebra*.—Krüger, 1922 [listed, taxonomy].

*Notopsychops zebra*.—Tillyard, [1919a] [taxonomy]; Kimmins, 1939 [listed, distribution, wing*].

FLIGHT PERIOD: 29 October - 8 May. MATERIAL EXAMINED [4M, 14F, 1? = 19]: **KENYA:** 1M, 2

mi. E. Taveta [3°24′S, 37°41′E], 29.x.1957, 840m, Ross & Leech (CAS); 1F, Kenya coast, Sokoke forest [station = 3°29′S, 39°50′E], 8.v.[19]76, Bampton (MINTER); 1M, 3F, Kilifi [3°38′S, 39°51′E], Sokoke forest, iv.1958, iv.1960, iv.1962, Williams (NMK); 2F, Coast Prov., Kilifi, Sokoke forest, iv.1957, 200ft., Williams (NMK); 1F, Sokoke For[est], White Sand, 8 mi. S. Malindi [3°13′S, 40°07′E], iv.1969, Clifton (NMK); 1F, 1?, Kibwezi [2°25′S, 37°58′E], 22.xii.[19]24, 16.i.[19]26, Feather (BMNH); 1M, 2F, Kasigau [3°49′S, 38°40′E], xi.1938, ?van Someren (BMNH); 1F, nr. Teita [=?Taita Hills, 3°25′S, 38°20′E], i.1892, 2500-3000′, Jackson (BMNH). **TANZANIA:** 3F, G[erman] E[ast] Africa, Rd to Kilossa [=Kilosa, 6°50′S, 36°59′E], Usagara Dist., 22-26.xii.1910, 1500-2500ft, Neave (BMNH); 1M, D[eutsch] O[st] Afrika, D[?]eymer (ZMHB).

**leoninus** Navás, 1910: south-central and southeastern Africa (Note: Many early records of "zebra" pertain to this species).

[*Psychopsis zebra*].—Gerstaecker, [1894] [redescription, distribution]; Navás, 1929 [listed, distribution]; Navás, 1931 [listed, distribution]; Esben-Petersen, 1936 [listed, distribution].

*Zygophlebius leoninus* Navás, 1910:83 [original description, forewing*].

*Psychopsis felina* Navás, 1912a:111 [original description, male terminalia*].

*Zygophlebius zebra* var. *felina* [sic].—Navás, 1917 [redescription, distribution].

*Zygophlebius zebra* var. *leonina* [sic].—Navás, 1917 [redescription, distribution].

*Zygophlebius zebra* var. *weelina* [sic] Navás, 1917:203 [original description].

[*Nothopsychops* (sic) *zebra*].—Tjeder, 1960.

[*Notopsychops zebra*].—Handschin & Markl, 1955 [listed, distribution]; Tjeder, 1960 [redescription, distribution, male terminalia*, female terminalia*, wing*, habitus*].

FLIGHT PERIOD: September (day unrecorded, see Handschin and Markl, 1955:67) - March (day unrecorded, see Tjeder, 1960:198). MATERIAL EXAMINED [73M, 81F, 27? = 181]: **ANGOLA:** 3F, Duque de Bragança [=Calandula, 9°06′S, 15°57′E], 29.x.1903, Hebel (RNHL); 1M, 1F, Bange Ngola [=?Bange Angola, 8°26′S, 16°40′E], 4.x.1903, Hebel (RNHL); 3M, 2F, 3?, Luacinga R[iver] [=?Luassing(u)a R., 15°44′S, 18°39′E], xi.[18]99, Penrice (RNHL, BMNH[1?], EMAU[1F]); 1F, 1?, Longa R[iver] [=?Luassingua

R.], xi.[18]99, Penrice (RNHL); 1M, Ndalla Ango, 12.x.1903, Hebel (RNHL); 1F, Gamba-Andulo, Bihé [=Kuito, 12°23′S, 16°56′E], xii.1934, Braun (BMNH); 2?, Angola S. or., Cacolo [10°09′S, 19°21′E] (westl. Saarimo), 23.xii.1957, 1400m, Heinrich (ZSM, identification based on photo & label data). **MALAWI:** 1F, Nkata Bay [=Nkhata Bay, 11°36′S, 34°18′E], Mkuwadzi Forest, 27.xi.1970 (NMB); 1F, Nyasaland, Mlanje [16°02′S, 35°30′E], 26.xi.[19]44, 2000ft., Wood (NMB); 3F, Nyasaland, Mlanje, 29.xi.1912, 29.i.1914, Neave (BMNH); 1?, Zomba [15°23′S, 35°20′E], ?Rendall (BMNH); 1F, Kasungu Nat. Park, Lifupa Camp [13°03′S, 33°09′E], 1333Aa, 9-10.xii.1980, 1000m, [ex.?] *Brachystegia*, Stuckenberg & Londt (NCIP); 1M, Kandoli [=?Kandoli Hill, 11°34′S, 34°16′E], lower slope, Nkata Bay Dist., Nyasaland, 16.xii.1960, ex. woodland, Eccles (NMB). **MOZAMBIQUE:** 1F, Rikatla [=?Lagoa Ricatla, 25°46′S, 32°37′E] (NHMW); 1M, 2F, Dondo Forest [Dondo, 19°36′S, 34°44′E], P[ortugese] E[ast] A[frica], xii.1960 (NMB); 2M, Beira [19°50′S, 34°52′E], 19.ii.[19]00 (BMNH); 1?, Delagoa Bay [=Baía de Lourenço Marques, 25°48′S, 32°51′E], Heyne (EMAU, no abdomen or original labels); 1F, Delagoabai [=Delagoa Bay], [pre-1894], Monteiro (ZMHB). **SOUTH AFRICA: TRANSVAAL:** 5M, 3F, Farm Murlebrook, nr. Tzaneen, 23°57′S, 30°10′E, 29.xii.1987, Scholtz or Minter (NCIP); 6M, 4F, Farm Murlebrook, Letsitele Valley, Tzaneen district, 4.xii.1988, densely wooded area near stream, Minter (MINTER); 5M, 3F, Hans Merensky Nat. Res., 23°40′S, 30°39′E, 27-30.xi.1981, Mansell or Oberprieler (NCIP, FSCA); 3M, 1F, Farm Glen Lyden, nr. Klaserie, 24°30′S, 30°57′E, 18.xii.1975, ex. forest along stream, Minter (MINTER); 1M, Farm Rietfontein, nr. Nelspruit, 25°24′S, 30°48′E, 14.xii.1975, ex. forest along stream, Minter (MINTER); 1M, Kruger Nat. Park, Skukuza, 24°59′S, 31°55′E, 13.xii.1985, Braack (NCIP); 1F, Trichardsdal, 24°10′S, 30°24′E, 9.i.1982, ex. light, Oberprieler (NCIP); 2F, Farm Weltevreden, Nelspruit Dst., 25°34′S, 31°10′E, 1.ii.1989, at light, Oberprieler (NCIP); 1M, 1F, Montrose Falls, 25°25′S, 30°44′E, 29.i.1989, Oberprieler (NCIP); 1M, 1F, Duiwelskloof [23°42′S, 30°08′E], 13.i.1987, Eardley (NCIP); 1M, 1F, 7km N Hazyview, Sabie River, 6.xii.1976, Miller (NCIP); 1F, White River [=?Wit Kei River, 32°09′S, 27°24′E], E. Transvaal, i.[19]07, ?Distant

(BMNH); 1F, Mt. Chirinda[?], S. Africa, 14.xii.1908, 3800′, Swynnerton (BMNH); 1?, Ost Transvaal, Karino [=Carino, 25°28′S, 31°06′E], i.1911, Cooke (ZMHB). **SWAZILAND:** 1M, 1F, Mlawula, 26°11′S, 32°04′E, 16.xi.1989, stunted *Androstachys johnsonii* forest in Lebombo Mts. nr. Mbuluzi Riv., Minter (MINTER). **TANZANIA:** 3M, 4F, Mpanda district, Katuma-Mpanda road, ca. 6°10′S, 30°49′E, 25.xi.1971, ca. 1300m, Kielland (RNHL); 1F, Mpanda district, Mabu, Wanzizi [=Wansisi] Hills, ca. 6°26′S, 30°29′E, 22.xi.1966, 1200m, Kielland (RNHL); 2M, 1F, Mpanda district, Sibweza, ca. 6°27′S, 29°55′E, 6.i.1969, xii.1970, xii.1971, 1100m, Kielland (RNHL); 1M, Mpanda district, Utinta, ca. 6°21′S, 30°28′E, xii.1971, 1200m, Kielland (RNHL); 1M, Mpanda district, Kampisa River, 6°07′S, 30°36′E, 4.xii.1966, Kielland (RNHL); 1M, Mpanda [6°22′S, 31°02′E], 8.xii.1969, Kielland (RNHL); 1M, Kapanga [6°18′S, 30°35′E], 10.xii.1962, Kielland (RNHL); 1F, Mpanda, Kapanga, 10.xii.1962, Kielland (RNHL); 1F, Thelembi, 2.xii.1966, Kielland (RNHL); 3M, 3F, Songea [10°41′S, 35°39′E], Mawanga forest, xii.1969, Watulege (NMK); 3?, Tanganjika, Songea, Peramiho, 26.xi.1958, 1000m, Lindemann (ZSM, identification based on photo and label data); 1?, Kigonsera [10°48′S, 35°03′E], 1907 (ZSM, identification based on photo and label data); 1M, 1F, [German] East Africa, Tendaguru, 1.i.1925, Cutler (BMNH); 1M, 1F, D[eutsch] O[st] Afrika, Tendaguru, Janensch (ZMHB). **UGANDA:** 1F, Uganda, ex. McLachlan Coll. (BMNH). **ZAIRE (=Belgian Congo):** 1M, Muye [9°00′S, 26°43′E], Park Upemba, 17.i.[19]58, 1570m, Ross & Leech (CAS); 2F, 150-200mi. W. of Kambove [=?Kambove at 10°52′S, 26°38′E], 23.x.[19]07, 1.xi.[19]07, 3500-4500ft., Neave? (BMNH); 1F, S.E. Katanga, 4.xii.[19]07, 4000′, ?Neave (BMNH); 2M, 2F, 1?, Lulua: Kapanga [8°21′S, 22°35′E], 11.xi.1932, 21.xi.1932, x.1933, xii.1933, Overlaet (MRAC); 1M, 1F, 1?, Elisabethville [11°40′S, 27°28′E], x.1911, "Miss. Agric." (MRAC); 2M, 1F, Elisabethville-Lubumbashi, 9.xii.1923, xi.1926, Seydel (MRAC); 3F, 2?, Kafakumba [9°41′S, 23°44′E], x.1930, ii.1931, Overlaet (MRAC); 2M, 1F, 4?, Sandoa [9°41′S, 22°52′E], xi-xii.1930, Overlaet (MRAC); 1M, 1F, 1?, Lulua: Riv. Luiza [ca. 7°35′S, 22°40′E], x.1933, 18.x.1933, Overlaet (MRAC); 2M, 1F, Kalenge [or Lulua]: Tshibalaka [8°32′S, 23°13′E], 13.x.1933, x.1933, Overlaet (MRAC); 1F, Uelé:

Paulis [2°46'N, 27°37'E], 1946, Abbeloos (MRAC); 1M, Katanga: Sashila [ca. 9°40'S, 23°20'E], 26.x.[19]25, Overlaet (MRAC); 1F, Rutschuru [1°11'S, 29°27'E], i.1928, Seydel (MRAC); 1M, Mufungwa Sampwe [9°20'S, 27°26'E], 20.xi.1911, Bequaert (MRAC). **ZAMBIA (=N. Rhodesia):** 1M, Chisamba, nr. Lusaka, 14°58'S, 28°15'E, 5-24.xii.1989, ex. light trap, Reavell (NMSA); 2F, Kasanka Nat[ional] Game Res[erve], Lake Wasa Camp, 12°30'S, 30°15'E, 14-22.xii.1989, ex. light trap, Reavell (NMSA); 1M, Abercorn [=Mbala, 8°50'S, 31°22'E], i.1967 (NMK); 1F, Abercorn, 13.i.1964 (NMB); 2M, 2F, 1?, Kitwe [12°49'S, 28°13'E], xi.1961, xii.1961, 8.xii.1961 (NMB); 1F, Ikelenge [11°14'S, 24°16'E], Mwinilunga [11°44'S, 24°26'E], 18.i.1965 (NMB); 2F, Ndola [12°58'S, 28°38'E], 4.i.1954, Cottrell (UZIL); 1F, Kasempa [=? 13°27'S, 25°50'E], 7.xii.[19]59, Johnsen (NMB); 1?, N'Sombo [10°49'S, 29°56'E], N. of Lake Bangweulu, 11.xii.1946, ex. low forest (BMNH); 1?, Kipushi [12°48'S, 30°43'E], N. Rhodesia: Congo Border, 15.xii.1927, ex. light, Evans (BMNH). **ZIMBABWE (=S. Rhodesia):** 3M, 1F, Burma Valley, Mutare district, 19°12'S, 32°42'E, 19.xi.1990, forest, Minter (MINTER); 2F, Vumba Mts., Umtali [18°58'S, 32°40'E], i.1960 (NMB); 3M, 1F, Witchwood Valley, Vumba Mts., Umtali, i.1960 (NMB); 1F, Haroni River [20°01'S, 33°01'E], xi.1967, ?Melsetter (NMB); 1F, Mashonaland [=NE Zimbabwe], 13.i.[18]96, Marshall (BMNH); 1M, Umtali District, 8.xii.1931, Sheppard (NCIP); 1M, Umtali, Mashonal'd, 25.?.1900, Marshall (BMNH). **UNCERTAIN IDENTIFICATIONS** (terminalia lacking, associations based on collection localities): **SOUTH AFRICA: NATAL:** 1?, Pongola River, N. Zululand, 20.x.[19]38, Marly (SAMC). **ZIMBABWE:** 1?, S. Rhodesia, Vumba, Umtali, i.1946 (NMK).

## Subfamily PSYCHOPSINAE Handlirsch
### Genus **BALMES** Navás

**terissinus** Navás, 1910: southeast Asia  **New Status**

*Balmes terissinus* Navás, 1910:85 [original description, forewing*].—Navás, 1917 [redescription].

TAXONOMIC NOTE: *Balmes terissinus* is here resurrected from synonymy with *birmanus* (e.g., New, [1989a]). Justification for this change is documented above in the taxonomic treatment of the genus *Balmes*.

FLIGHT PERIOD: April (day unrecorded)-21 July. MATERIAL EXAMINED [18M, 3F, 5? = 26]: **CHINA: SZECHWAN PROVINCE:** 1?, Suifu, 30.v.1925, 2000ft., Graham (MCZ); 17M, 4?, Yunnan border S of Suifu, iv.[19]29, Graham (MCZ, USNM); 1F, Chengtu, 21.v.1929, Parish? (CUIC); 1M, 1F, Chengtu, v.1934, Graham (MCZ, USNM); 1F, Mt. Omei, 21.vii.[19]35, 4000ft., Graham (USNM).

**birmanus** (McLachlan, 1891): southeast Asia

*Psychopsis birmana* McLachlan, 1891: 320 [original description].—Krüger, 1922 [listed]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

*Balmes notabilis* Navás, 1912b:197 [original description].—Navás, 1917 [redescription].

*Balmes birmanus* (-a [sic]).—Navás, 1930 [listed, distribution]; Kimmins, 1939 [listed, distribution].

FLIGHT PERIOD: April (days unrecorded). MATERIAL EXAMINED [3M, 1F = 4]: **CHINA: YUNNAN PROVINCE:** 1M, bet. Tengyueh and Nan Tien, "1909-10," Brown (CUIC). **UNKNOWN PROVINCE:** 2M, Yun Hsien, iv.1942, Jellison (USNM); 1F, Loimwe [? Loirnwe], iv, 5-6000', Kingford (MCZ).

**bns1** (=*Balmes* new species #1; undescribed): southern China

FLIGHT PERIOD: 2 June. NOTES: Females unknown; known only from the unique male below. MATERIAL EXAMINED [1M]: **CHINA:** 1M, Kunming, 2.vi.1941 (USNM).

**formosa** (Kuwayama, 1927): Taiwan (Note: The specific name *"formosa"* is treated here as a noun in apposition, Art. 31b(ii).).

*Psychopsis (Orientichopsis) formosa* Kuwayama, 1927:123 [original description, habitus*].

*Balmes formosana* [sic].—Kimmins, 1939 [listed, distribution].

*Psychopsis formosa.*—New, [1989a] [redescription, distribution, female terminalia*, wing*].

FLIGHT PERIOD: August (see Kuwayama, 1927:125). NOTES: Males unknown; known only from the two females (not males as stated by Kuwayama, see New, [1989a]:846) of the type series. MATERIAL EXAMINED: None.

## Genus **PSYCHOPSIS** Newman

### *coelivaga* species group

**coelivaga** (Walker, 1853): northeastern Australia [Queensland, ?Victoria]

*Hemerobius coelivagus* Walker, 1853:279 [original description].

*Psychopsis coelivaga* (-us [sic]).—McLachlan, 1863 [listed]; Hagen, 1866 [listed]; Brauer, 1889 [listed]; Froggatt, 1903 [redescription, distribution, habitus*]; Tillyard, [1919a] [listed, distribution]; Krüger, 1922 [listed]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

*Wernzia caelivaga* [sic].—Navás, 1912b [redescription, distribution, wing*]; Navás, 1917 [redescription].

*Wernzia coelivaga* (-us [sic]).—Kimmins, 1939 [listed, distribution].

FLIGHT PERIOD: 23 October - 28 February [Outlier: May (day unrecorded)]. MATERIAL EXAMINED [7M, 5F, 6? = 18]: **AUSTRALIA: QUEENSLAND:** 1F, Toowoomba, 5.i.[19]42, Common (UQIC); 4M, Killarney, 24.ii.[19]46, 6.i.[19]50, Dumigan (UQIC); 1?, Killarney, 28.ii.[19]50, Morris (UQIC); 1?, Kuranda, Dodd (SAMA); 1?, Range Hallanton?, 22.xii.[19]12, Beck (UQIC); 1?, Brisbane (SAMA); 1F, Brisbane, 23.x.[19]21, Hacker (QMB); 1F, Herberton, 15.i.1911, Dodd (MCZ). **VICTORIA:** 1F, Horsham [?adventitious, see New [1989a]: 853] (SAMA). **UNKNOWN STATE:** 1F, Masdore?, 2.xi.[19]13, Buialing? (UQIC); 3M, 1?, Towbu, 1.ii.[19]20, 4.xii.[19]21, Beck (QMB, UQIC); 1?, Mt. Nebo, v.[19]50, Edye (UQIC).

### *insolens* species group

**insolens** McLachlan, 1863: eastern Australia [New South Wales, Queensland]

*Psychopsis insolens* McLachlan, 1863:114 [original description, habitus*].—Hagen, 1866 [listed]; Brauer, 1889 [listed]; Froggatt 1902 [listed]; Froggatt, 1903 [listed, distribution, habitus*]; Tillyard, [1919a] [listed, distribution]; Krüger, 1922 [listed]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

[*Psychopsis coelivagus* (sic)].—Froggatt, 1902 [listed].

*Magallanes insolens.*—Navás, 1917 [redescription, wing*]; Kimmins, 1939 [listed, distribution].

FLIGHT PERIOD: 16 November - March (day un-

recorded). MATERIAL EXAMINED [37M, 23F, 10? = 70]: **AUSTRALIA: NEW SOUTH WALES:** 2F, 1?, Beecroft, 17.i.[19]63, 7.xii.1967, 22.i.1971, Williams (DANSW); 1F, Collaroy, 7.i.1962, Gaven (DANSW); 1F, Glenhaven, 8.ii.1988, Davison (DANSW); 1M, Erina Heights, 17.xii.1981, Holtkamp (DANSW); 1F, Ourimbah, iii.1986, Adamski (DANSW); 1F, Narara, 15.xii.1944, Riely (DANSW); 1F, Lindfield, ii.1911, Fry (AMS). **QUEENSLAND:** 14M, 1F, 5?, Killarney, 4.xii-27.i/1923-1952, mostly ex. Dumigan collection (UQIC, QMB); 5M, Toowoomba, 25.xi-25.xii/1919-1929, various coll. (UQIC); 2M, 1F, 1?, Brisbane, 16.xi-24.i/ 1920-1938, (UQIC, QMB); 1F, 1?, Stanthorpe, 19.i.[19]26 (UQIC); 1M, Burleigh [20°17'S, 143°05'E], 29.xi.[19]26 (UQIC); 1M, Glen Aplin, i.1963, at light, Elder (UQIC); 1F, Ferny Groove, 24.xi.[19]62, Lisle (UQIC); 13M, 11F, Canungra, xi.1965, 8-17.xii.1966, Curtis (UQIC). **UNKNOWN STATE:** 1F, "Nord Australia / 1864" (MCZ); 1?, no data (UQIC); 1?, Darlington, 1.xii.[19]46, Rosser (UQIC).

**meyricki** McLachlan, 1887: eastern Australia [New South Wales]

*Psychopsis meyricki* McLachlan, 1887:30 [original description].—Brauer, 1889 [listed]; Tillyard, [1919a] [listed, distribution]; Krüger, 1922 [listed]; New, [1989a] [redescription, distribution, male terminalia*, wing*].

*Magallanes meyricki.*—Navás, 1917 [redescription]; Kimmins, 1939 [listed, distribution].

FLIGHT PERIOD: 20 January. NOTES: Females unknown; known only from the seven males of the type series. MATERIAL EXAMINED [3M]: **AUSTRALIA: NEW SOUTH WALES:** 3M, "Mt. Kosciusko" [more specifically, Jindabyne, see Tillyard, [1919b]: 779], 20.i.1885, 2800ft., paratypes, [Meyrick, see orig. desc.] (BMNH).

### *illidgei* species group

**illidgei** Froggatt, 1903: eastern Australia [New South Wales, Queensland]

*Psychopsis illidgei* Froggatt, 1903:455 [original description, distribution, habitus*].—Navás, 1917 [redescription, wing*]; Krüger, 1922 [listed].

*Megapsychops illidgei.*—Tillyard, [1919a] [redescription, distribution, ?female terminalia*, wing*, habitus*]; Tillyard, 1926 [habitus*]; Kimmins, 1939 [listed, distribution]; New, [1989a] [rede-

scription, distribution, male terminalia*, female terminalia*, wing*].

FLIGHT PERIOD: 12 December - 3 January. MATERIAL EXAMINED [1M, 3F = 4]: **AUSTRALIA: QUEENSLAND:** 1F, Mt. Tambourine, Geissmann (AMS); 1F, Mt. Tambourine, 12.xii.1942, 1200', Tisdale (SAMA); 1F, Mt. Tambourine, xii.1944 (QMB); 1M, Bunya Mts., 3.i.1945 ["3-1-45"], Dumigan (UQIC).

### *gracilis* species group

**gracilis** Tillyard, 1919: eastern Australia [New South Wales, Queensland]

*Psychopsis gracilis* Tillyard, [1919a]:776 [original description, ?female terminalia*, wing*, habitus*].—Kimmins, 1939 [listed, distribution]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

FLIGHT PERIOD: 26 October - 30 January. MATERIAL EXAMINED [3M, 1F = 4]: **AUSTRALIA: QUEENSLAND:** 1M, 15 mi. SW Burleigh Hds., 26.x.1962, 50m, Ross & Cavagnaro (CAS); 1M, Killarney, 30.i.[19]52, Morris (UQIC); 1?, Tambourine Mts., Pa[u?]ttinson (QMB). **QUEENSLAND or NEW SOUTH WALES:** 1M, Macpherson Ra[nge], 28.xii.[19]41, D[umigan] (UQIC).

**elegans** (Guérin-Ménéville, [1844]): eastern Australia [New South Wales, Queensland]

*Artiopteryx elegans* Guérin-Ménéville, [1844]:389 [original description].—Erichson, 1847 [redescription].

*Psychopsis elegans.*—Hagen, 1866 [listed]; Brauer, 1889 [listed]; Tillyard [1919a] [listed, distribution, wing*]; Tillyard [1919b] [biology, egg*, larval instars*, pupa*]; Krüger 1922 [listed]; Gallard 1923 [note]; Tillyard 1926 [habitus*]; Kimmins 1939 [listed, distribution]; New [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

[*Psychopsis mimica*].—Froggatt, 1902 [redescription, 1st instar larva].

*Psychopsis newmani* Froggatt, 1903:454 [original description, distribution, habitus*].—Gallard, 1914 [biology]; Navás, 1917 [redescription, distribution].

*Zygophlebius verreauxinus* Navás, 1910:84 [original description, wing*].

*Arteriopteryx* [sic] *elegans.*—Navás, 1917 [redescription].

FLIGHT PERIOD: 14 October - 24 January. MATERIAL EXAMINED [12M, 8F, 3? = 23]: **AUSTRALIA: QUEENSLAND:** 1M, Cairns dist., Dodd (SAMA); 1F, 1?, Toowoomba, Barnard (QMB); 1M, 1?, Brisbane, 20.x.[19]25, 12.xii.[19]39 (UQIC, QMB); 4M, Kuranda, Dodd (SAMA); 1M, Yeppoon, 14.x.[19]24 (QMB); 1M, no further locality, 1844, Thorey (MCZ); 1M, Bulimba, 28.x.[19]09 (USNM); 1F, Biloela [24°21'S, 150°30'E], 11.xii.[19]46, Bird (UQIC); 1M, Biloela, 24.i.[19]45, Rosser (UQIC); 1F, Bundaberg [24°50'S, 152°21'E], 25.x.[19]32 (UQIC); 1?, Wacol [27°35'S, 152°56'E], 18.xii.[19]51, Box? (UQIC). **NEW SOUTH WALES:** 1F, Sydney, Summe Hill, 2.i.[19]13, Downing (DANSW); 1M, Eppine, 24.xii.[19]15, reared, Tillyard (SAMC); 1M, Warialda district, xii.1949 (DANSW). **UNKNOWN STATE:** 2F, no locality data, 16-19.xii.[19]40, (UQIC); 1F, no data (USNM); 1F, Ft. Denison, N. Australien, 1847, Daemel (MCZ).

**mimica** Newman, 1842: eastern and southern Australia [New South Wales, s. Northern Territory, Queensland, South Australia, Victoria, Western Australia]

*Psychopsis mimica* Newman, 1842:415 [original description].—Newman, 1843 [redescription, habitus*]; McLachlan, 1863 [listed]; Hagen, 1866 [listed]; Brauer, 1889 [listed]; Froggatt, 1903 [redescription, distribution, habitus*]; Navás, 1917 [redescription]; Tillyard, [1919a] [listed, distribution]; Gallard, 1922 [biology]; Krüger, 1922 [listed]; Gallard, 1923 [biology]; Tillyard, 1926 [habitus*]; Kimmins, 1939 [listed, distribution]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].

*Hemerobius mimicus.*—Walker, 1853 [redescription, distribution].

*Hemerobius olim* Brauer, 1889:103 [nomen nudum].

[*Psychopsis elegans*].—Kimmins, 1939 [wing*].

FLIGHT PERIOD: 14 October - 11 March. MATERIAL EXAMINED [9M, 57F, 8? = 74]: **AUSTRALIA: NEW SOUTH WALES:** 2M, 2F, Narrabri A.R.Stn., 24.xi.1966, 5-11.xi.1967, 1.xii.1967, some ex. light, Wright (DANSW); 1F, Narrabri, 24.i.1960, Lola (DANSW); 1F, Hay WWF, 20.i.1916 (DANSW); 1F, Tumut, 6.ii.1957, Nicholson (DANSW); 1F, Warren, i.1963, Grund (SAMA); 1F, Binnaway, 5.i.1934, Field (AMS); 1F, Deniliquin, 13.ii.1950 (DANSW); 1?, Coonabarabran [31°16'S, 149°18'E], 31.i.[19]47 (DANSW). **NORTHERN TERRITORY:** 1M,

Alice Springs, Ernabella Mission, 7.xi.1961, Hilliard (SAMA). **QUEENSLAND:** 1F, Cunnamulla, xi.1943, Geary (QMB); 2F, Cunnamulla, i.1941, 14.xii.1944 (QMB); 1F, St. George, i.1944, Geary (AMS); 2F, 1?, Clermont [22°48'S, 147°40'E], 14.x.[19]23, 21.x.[19]24, 26.ii.[19]24 (QMB, UQIC). **SOUTH AUSTRALIA:** 2F, Windy Cr. below Aroona Dam, 10km SW Copley, 24.xi.1975, ex. light, Gross (SAMA); 1F, Berri (SAMA); 2F, Berri, xii.1920, Hoskin (SAMA); 1M, 3F, no further locality (SAMA); 1F, Waikerie, i.1971, Doyle (SAMA); 1F, Balcanoona Ck., 23.xi.1975, ex. light, Gross & Potezny (SAMA); 1F, Blackwoood, 11.iii.[19]69, ex. light, McFarland (SAMA); 2M, 6F, 2?, Adelaide, 1.ii.1893, 15.ii.[18]98, 7.i.[19]08, 26.x.[19]10, most no date, various coll. (MCZ, SAMA); 1?, Wentworth, 19.i.[18]91 (SAMA); 1F, Wentworth, 21.ii.[18]93, Cudmore (SAMA); 1?, Reed Beds, ii.1894, White (SAMA); 1F, Reed-Beds, i.1903, Smith (SAMA); 1F, Reed-Beds, ii.1903, Jones (SAMA); 1F, Flinders Range, Mt. Painter, Stokes (SAMA); 1M, Laura, ii.[19]67, Peck (SAMA); 1F, Manoora, Kelly (SAMA); 1F, Unley Park, 26.ii.1961, ex. light, Southcott (SAMA); 2F, Waterfall Gully, 29.i.1948 (SAMA); 1F, Melrose, Shields (SAMA); 3F, Holmfirth, Fulham, ii.1898, ii.1899, i.1904, Mellor (SAMA); 1F, College Town, iii.1956, Melrose (SAMA); 1F, Murray Bridge [35°10'S, 139°17'E], Mackintosh (SAMA); 1F, Mitcham, 21.xii.[19]06, (SAMA). **VICTORIA:** 1F, Loddon Riv., 13.i (USNM); 1M, Gunbower, 2.ii.[19]54, Harley (UQIC). **WESTERN AUSTRALIA:** 1?, Beverley (SAMA). **UNKNOWN STATE:** 1F, Grumbungee (UQIC); 1F, G[rum]bungee, 27.xii.[19]20, Beck (UQIC); 1M, 1F, Madowla Park, 21.i (SAMA); 1F, no data (MCZ); 1F, Mt. Larcom, xi.1928, Chapman (QMB); 1F, "Australia / Angus" (MCZ); 1F, Jrura?, 19.xii.[19]00, Lewis (SAMA); 1F, Umberatana?, 8.xii.[18]99, Greenwood (SAMA); 1F, Renworth?, 22.xii.[18]92, (SAMA); 1?, "Australia" (MCZ); 1F, no data (SAMA).

**barnardi** Tillyard, 1925: northeastern Australia [Queensland]
*Psychopsis barnardi* Tillyard, 1925:388 [original description, habitus*].—Kimmins, 1939 [listed, distribution]; New, [1989a] [redescription, distribution, male terminalia*, female terminalia*, wing*].
FLIGHT PERIOD: 4-8 December. MATERIAL EX-

AMINED [18M, 3F, 2? = 23]: **AUSTRALIA: QUEENSLAND:** 12M, 1?, "Carnavon" [=Carnarvon?] Range, xii, Geary (MCZ); 2M, 1?, Carnarvon Range, 4-6.xii.[19]41, Franzen (UQIC); 4M, 1F, Carnarvon Range, 5-8.xii.1941 (QMB); 1F, no data [Queensland?] (UQIC); 1F, Brisbane, [19]52, "RPK" (UQIC).

**tillyardi** New, [1989]: north central Australia [Northern Territory]
*Psychopsis tillyardi* New, [1989a]:851 [original description, distribution, female terminalia*, wing*].
FLIGHT PERIOD: 11 April (see New, [1989a]:851). NOTE: Males unknown; known only from the female holotype and the following specimen. MATERIAL EXAMINED [1F]: **AUSTRALIA: NORTHERN TERRITORY:** 1F, Bathurst Is. (SAMA).

**dumigani** Tillyard, 1922: northeastern Australia [Queensland]
*Psychopsis dumigani* Tillyard, 1922a:36 [original description, A*, habitus*].—Kimmins, 1939 [listed, distribution]; New, [1989a] [redescription, distribution, female terminalia*, wing*].
*Psychopsis notha* Navás, 1928:65 [original description, distribution, forewing*].
FLIGHT PERIOD: 1-11 November (see Tillyard, 1922a:36). NOTES: Males unknown; known only from ca. six female specimens. Males previously cited by Tillyard are actually females, see New, [1989a]:852. MATERIAL EXAMINED: None.

**maculipennis** Tillyard, 1925: western Australia [Western Australia]
*Psychopsis maculipennis* Tillyard, 1925:389 [original description, habitus*].—New, [1989a] [redescription, distribution, wing*].
*Wernzia maculipennis.*—Kimmins, 1939 [listed, distribution].
FLIGHT PERIOD: Unknown (unique holotype lacks temporal collection data). NOTES: Males unknown; known only from unique female (not male as stated by Tillyard, see New, [1989a]:852) holotype. MATERIAL EXAMINED: None.

**margarita** Tillyard, 1922: eastern Australia [New South Wales]
*Psychopsis margarita* Tillyard, 1922a:37 [original description, habitus*].—Kimmins, 1939 [listed, dis-

tribution]; New, [1989a] [redescription, distri-
bution, female terminalia*, wing*].
FLIGHT PERIOD: 29 December (see Tillyard,
1922a:38). NOTES: Males unknown; known only
from the two females (not males as stated by
Tillyard, see New, [1989a]:850) of the type se-
ries. MATERIAL EXAMINED: None.

PSYCHOPSINAE *incerta sedis*

**gallardi** (Tillyard, 1919): eastern Australia [New
South Wales, Queensland]
*Psychopsella gallardi* Tillyard, [1919a]:780 [original
description, male terminalia*, wing*,
habitus*].—Gallard, 1923 [listed, distribution].
*Balmes gallardi*.—Kimmins, 1939 [listed, distribu-
tion].
*Psychopsis gallardi*: New, [1989a] [redescription, dis-
tribution, male terminalia*, wing*].
FLIGHT PERIOD: 7 December - 14 January (see
New, [1989a]:847). NOTES: Females unknown;
known only from two male specimens. MATE-
RIAL EXAMINED [1?]: **AUSTRALIA:**
**QUEENSLAND:** 1?, Carnarvon Range,
7.xii.1941 (QMB). [This specimen is tentatively
identified as gallardi. Its forewing markings are
similar to those illustrated by Tillyard ([1919a]:
plate 78, fig. 11), and it lacks a distal hind wing
macula. However, the costal gradate series of
the specimen are much more complete (18
crossveins in each wing) than is indicated by
either Tillyard or New ([1989a]) for the other
known specimens of this species. This specimen
was not included in the cladistic analysis be-
cause it lacks an abdomen.]

# APPENDIX 2

## Character State Data Matrix

The coded character state data in the matrix below were used to infer cladistic relationships within the family Psychopsidae. The data shown for the ingroup taxa and the hypothetical ancestor were used to generate the cladogram shown in Fig. 53. The data shown for the outgroup taxa are presented only to document the assignment of ground plan character states to the hypothetical ancestor (see Phylogenetic Analysis: Methods above); these data were not included in the final cladistic analysis. Characters, character states, and outgroup taxa are discussed more fully in the text. Derived character states which were found to be restricted to outgroup taxa (matrix code "-") have been omitted from the textual character treatments. These omissions have been verified to have no affect on the character states assigned to the hypothetical ancestor. Symbols: 0-4, character state numbers; ?, missing ingroup data (i.e., relevant sex unknown or not seen and data not available in the literature); *, state uncoded due to uncertain ingroup/outgroup homology; -, derived state restricted to one or more outgroup taxa, individual states not treated in text.

| Taxon | Character Number |
|---|---|
| | 0000000001111111112222222222 3333333333344444444445555555556 |
| | 1234567890123456789012345678 901234567890123456789012345678 90 |
| **Outgroup Taxa** | |
| *Agulla* | - 000000000000- 0000000100000001- 00000000000*00000- 1000010000 |
| *Halter* | 20000000000000000- 0001001000 01101000- 0000000000000000000000 |
| *Kempynus* | - 00000000- 00000000001000000* ********000000- 0000010000010000 |
| *Nomerobius* | 20000000000000000- 0- 1- 000000 1000000000000- 0000000000010000 |
| *Nymphes* | - 0001000000000000000100000000- 110000000000- 0000001000010000 |
| *Osmylops* | 20001000000000000- 0000000000 0- 000000002000- 0000001000010000 |
| *Osmylus* | - 00000000- 00000000000000000* ********00- 000- 0000010000010000 |
| *Polystoechotes* | 2000000000000010- 0111000- 00 01000000000000- 0000000000010000 |
| | |
| **Hypothetical Ancestor** | |
| HypAnc | 0000000000000000000010000000 0100000000000000000000000010000 |
| | |
| **Ingroup Taxa** | |
| *P. barnardi* | 1010112121000120222100121002 0011000111011103211111012110011 |
| *B. birmanus* | 1000100102000120100011140010 0011000210110112011111002100001 |
| *P. coelivaga* | 2000110110000120104001010000 0011000210010102011111012110001 |
| *P. elegans* | 1010112121000120222100130001 0011000211010103111111012110011 |
| *C. gloriosus* | 1100111101110110100001000000 0101001100101011111002110101 |
| *P. gracilis1* | 1010112121000120112011110001 0011001101?103?1???1101?1??0?? |
| *P. illidgei* | 1000112111000120113011110102 0021000211101130111111012110011 |
| *P. insolens* | 1000112131000120100001110000 0011000211110102011111012110001 |
| *S. jordani* | 0100111101000111101001100000 0100011001010201111111101110201 |
| *Z. leoninus* | 1101112141100110101002100000 101001111002010101111111002121101 |
| *S. marshalli* | 0100111101001111101001100000 20000011001010201111111101110201 |
| *P. meyricki2* | 1000112131000120100001110000 0110002110?????????????????????? |
| *P. mimica* | 1010112121000120222100121001 0011000211010103111111012110011 |
| *S. occultus* | 0100111101001111101001100000 20000011001010201111111101110201 |
| *S. rufus3* | 0100111101001111101001100000 10000011001010?0??1?111011??20? |
| *B. terissinus* | 1000100102000120100011140000 0011000210110112011111002110001 |
| *P. tillyardi4* | 1010112121??????????????????? ??????????1110321111111012110011 |
| *Z. zebra* | 1101112141100110101002100000 101001111002010101111111002121101 |
| bns15 | 1000100101000120101011140110 0011000210101?????????????????? |
| cns1 | 1100111101110110100001000000 0101001001010101111111002110101 |
| zns1 | 1101101141100110100002100000 010010110020101011111002111101 |

[1] Female not seen, incomplete female terminalia data taken from New ([1989a]: figs. 75-79).
[2] Female unknown (New [1989a]:854).
[3] Female not seen, incomplete female terminalia data taken from Tjeder (1960: